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ERRATA

p. 284, line 7, for *Tosnsuoria* read *Tossunoria*.

p. 358, line 15 from bottom, for *ceylonicus* read *ceylanicus*.

p. 434, line 24, for *Harmonthoe* read *Harmothoe*.

p. 443, line 19, for **Eusllis** read **Eusyllis.**

p. 471, line 14 from bottom, for *Clyclopterus* read *Cyclopterus*.

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(ZOOLOGY)

The anatomy of *Ophioica asymmetrica*, sp. n., a Copepod endoparasitic in an Ophiuroid.

By K. A. Pyefinch, B.A. (Communicated by Dr. W. T. Calman, C.B., F.R.S., F.L.S.)

(With 12 Text-figures)

[Read 1 February 1940]

Introduction.

This paper gives a brief description of the external and internal anatomy of a new species of the Copepod genus *Ophioica* (Stephensen, 1933), which was found within the Ophiuroid *Ophiacantha imago* (Lyman, 1882). I propose to call this new species *Ophioica asymmetrica*. Through the kindness of Dr. Isabella Gordon, I have been able to examine three specimens of this Copepod, which were obtained from two specimens of the host Ophiuroid. The latter came from the Southern Indian Ocean and the Ross area, namely :—

'Challenger.' Stn. 150, lat. 52° 4′ S., long. 71° 22′ E. 150 fms., February 2nd, 1874 (containing one specimen of the Copepod).

'Discovery.' Stn. No. 5.9.14–17. Winter Quarters (Ross Sea area), 1907 (containing two specimens of the Copepod).

The occurrence of Copepods as endoparasites of Ophiuroids is rather rare. Stephensen (1933) quotes :—

Philichthys amphiurae (Hérouard, 1906).

Chordeumium obesum (Jungersen, 1912).

Arthrochordeumium appendiculosum (Stephensen, 1918).

References to these species are given in Mortensen and Stephensen (1918). To these must be added (Stephensen, 1933, 1935) :—

Arthrochordeumium asteromorphae (Stephensen, 1933).

Ophioica ophiacanthae (Stephensen, 1933).

Ophioica appendiculata (Stephensen, 1935).

Most frequently, only the external features of these parasites have been examined, purely from a taxonomic point of view. Since the present material

proved suitable for sectioning, some of the details of the internal anatomy could also be made out and it therefore seemed of interest to give this brief account of that anatomy.

General relationships with the host.

When the material was received for examination, the Copepods had been removed from their hosts, but it is probable that their position within the Ophiuroid is the same as that of *Ophioica ophiacanthae* within *Ophiacantha severa*, namely, inter-radial and within one of the bursae (Stephensen, 1933). The presence of the parasite within causes a slight swelling of the aboral surface of the Ophiuroid and in preserved specimens this is the only sign of infection with *Ophioica*. In the present material it was not possible to ascertain the effects of the presence of the Copepod more precisely, but it is clear that there is some considerable reaction on the part of the host, as the parasite is firmly embedded in a mass of Ophiuroid tissue which closely invests the surface of the Copepod and its processes and thus forms a rough 'cyst' around the latter (figs. 1, 5, 12, *o.t.*). Stephensen (1935) mentions that *O. appendiculata* was fixed to the wall of the bursa of its host, *Ophiomitrella clavigera* (Ljungman).

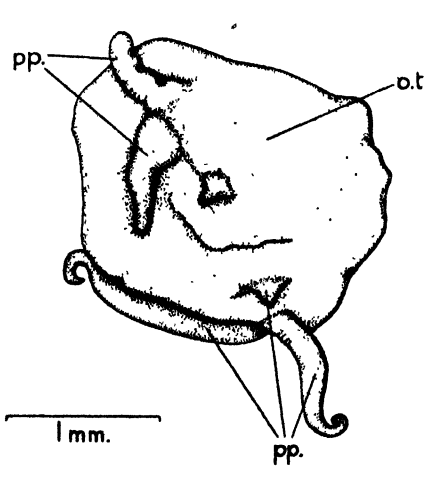

Fig. 1.—External features of *Ophioica asymmetrica*, after removal from the host.

o.t., ophiuroid tissue ; *pp.*, processes of parasite.

Because of this investing sheath of Ophiuroid tissue, little can be gathered from the external appearance of the parasite after removal from the brittle star. All that can be seen is a spherical mass of tissue, roughly 2 mm. in diameter, with, here and there, processes projecting from the central mass (fig. 1, *pp.*). Some of these processes are long and finger-like, and appear to be arranged in pairs, others are more papilliform. These processes arise from the

body of the Copepod and project out through the investing Ophiuroid tissue. Stephensen was able to dissect away the host-tissue from the surface of the parasite, but in this case it appeared impossible to remove the dense, rather fibrous Ophiuroid tissue from the delicate chitinous exoskeleton of the Copepod without injury to the latter, so that all the diagrams given below of the external features of the parasite are from models reconstructed from serial sections.

Of the three specimens available, two (from the 'Discovery') were examined in serial section; the remaining specimen (from the 'Challenger') being left intact as a type-specimen. Each of the two specimens examined in detail consisted of a male and female embedded together within the host-tissue, but in one case the female was ovigerous and in the other non-ovigerous. Correlated with these differences in the females, there were considerable differences in the degree of development of the males. In view of these differences in both sexes the two specimens are therefore described separately below.

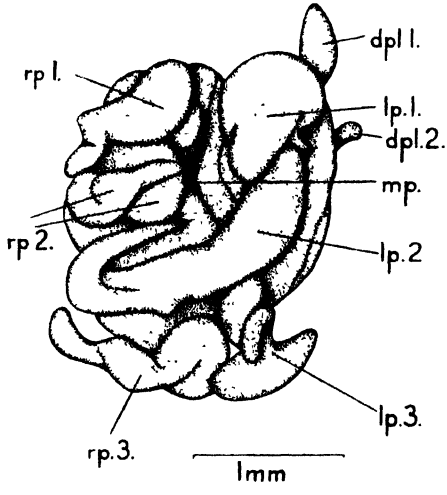

FIG. 2.—Ventral view of non-ovigerous female. From a reconstruction.
dpl. 1–2, left dorso-lateral process 1–2; *lp.* 1–3, left ventro-lateral process 1–3; *mp.*, 'median' process; *rp.* 1–3, right ventro-lateral process 1–3.

SPECIMEN 1.

This comprised the non-ovigerous female and a male which was practically mature.

(a) *The non-ovigerous female.*

(i) *External features.*

The external features of this individual are shown in fig. 2 (ventral view), fig. 3 (ventral view with the tips of the processes removed), and fig. 4 (dorsal view).

In ventral view three pairs of large serpentine processes can be seen. These arise ventro-laterally, but they are so pressed together by the investing Ophiuroid tissue that they project ventrally. The exact nature of these processes remains uncertain. It is possible that they may represent appendages, but a comparison with the similar processes of the body of the ovigerous female (see figs. 9 and 10, and p. 11, below) shows that there are considerable differences in their arrangement in the two individuals, so that it is more probable that they are simply processes of the body-wall, comparable, possibly, with similar processes present in other parasitic Copepods (e.g. *Philichthys xiphiae*, Wilson, 1932, p. 532, fig. 316). Because of this uncertainty these processes have simply been numbered as a convenience for descriptive purposes (fig. 2, *lp.* 1–3 ; *rp.* 1–3, etc.).

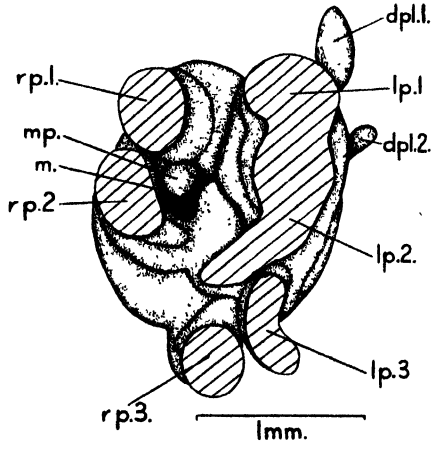

FIG. 3.—Ventral view of non-ovigerous female, with the tips of the processes removed. From a reconstruction.

m., mouth-region. Other lettering as before.

Between the processes of the left and those of the right hand side is a groove, approximately median in position, which is considerably deeper anteriorly. The male lies within this groove (fig. 6, *ma.*). Towards the anterior end of the groove and to its right-hand side is an unpaired, more median process, which can be seen more clearly when the tips of the paired processes have been removed (fig. 3, *mp.*). To the right of this process, opening between it and the base of the second process of the right-hand side, is the mouth (fig. 3, *m.*), which is thus asymmetrical in position.

In dorsal view the general appearance is more rounded (fig. 4), and from this aspect it can be seen that there is a further series of processes which arise dorso-laterally. On the left-hand side there are three of these, two anteriorly

and one towards the posterior end (fig. 4, *dpl.* 1–3), but on the right-hand side only two very small processes, situated anteriorly (fig. 4, *dpr.* 1, 2), can be made out.

In his description of *Ophioica appendiculata*, Stephensen (1935) gives diagrams (p. 16, fig. 9) of an adult non-ovigerous female, which would presumably correspond with the stage described above. In this specimen he thought that he was able to detect five segments and that an abdomen was present. Unless the ventro-lateral processes are truly appendages (which would indicate the presence of at least three segments) there are no traces of such segmentation in the non-ovigerous female of *O. asymmetrica*. There is no differentiation of a head region and there is no part of the body which can be recognised as abdomen.

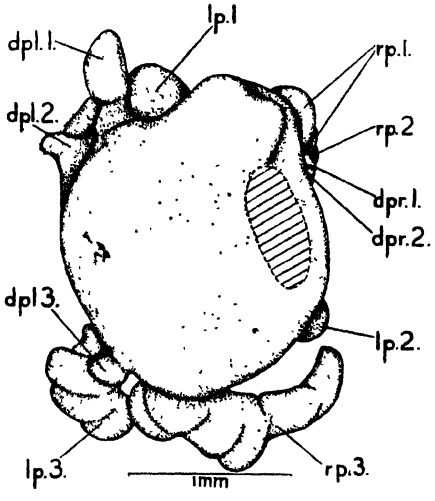

FIG. 4.– Dorsal view of non-ovigerous female. From a reconstruction. (The shaded area indicates the part torn off in the specimen examined.) *dpl.* 3, left dorso-lateral process 3; *dpr.* 1–2, right dorso-lateral process 1–2. Other lettering as before.

(ii.) *Internal anatomy.*

The only internal organs that are present are the alimentary canal and the ovary and oviducts.

The alimentary canal may be divided into fore- and mid-gut. These two regions are clearly differentiated, but if a hind-gut is present it is not to be distinguished from the mid-gut.

The fore-gut runs dorsally from the mouth to the mid-gut. The more ventral part of the fore-gut is lined with chitin (strong muscle-bands being attached to the outer walls of this chitinous lining), whereas the more dorsal part has

an epithelial wall. The mid-gut is much branched, and in this non-ovigerous female these branches, which penetrate some distance into the ventro-lateral processes, are compressed by the bulky oviducts (fig. 5, *g.b.*). Debris could be detected in the mid-gut, so that it appears probable that solid food is ingested.

The ovary and oviducts are by far the most conspicuous internal organs (fig. 5, *ovid.*), the former being an irregular lobed sac, tightly packed with ova and oocytes within. There is no clear boundary between the ovary and the first part of the oviduct. Both are thin-walled, and at the upper end of the oviduct are a few scattered ova not surrounded by yolk (compare fig. 12). This first part of the oviduct is much branched (the general plan of this branching

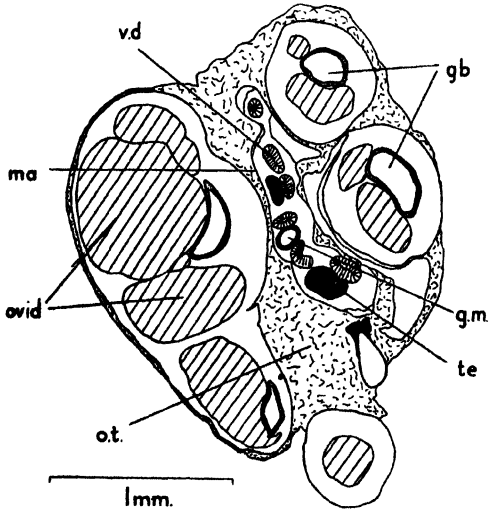

FIG. 5.—Horizontal section of non-ovigerous female, showing the male within the ventral groove of the female.

g.b., mid-gut branch of female ; *g.m.*, mid-gut of male ; *ma.*, male ; *ovid.*, oviduct ; *te.*, testis ; *v.d.*, vas deferens. Other lettering as before.

following that of the gut) and the cavities of all the branches are packed with the bulky yolk-laden ova. The details of this branching were not followed out completely.

The more ventral part of the oviduct differs completely from the dorsal part just described, as its wall is formed of a deep columnar epithelium. The appearance of this epithelium suggests that it is glandular in function and evidently this is the part of the oviduct which secretes the substance which binds the eggs together into the egg-masses. In this non-ovigerous female only one such glandular tubule could be detected. This runs ventrally for a short distance and then ends blindly.

(b) *The male.*

The spatial relationships of the male and female have already been partly described. Fig. 6 shows the male in position in the ventral groove of the female. The antero-posterior axis of the male lies practically at right angles to that of the female, so that a section cut horizontally through the female will cut transversely through the male (fig. 5). The male is completely embedded in the host-tissue which fills the ventral groove of the female, but though closely applied to the ventral surface of the latter the two individuals are not fused at any point.

The external form of the male is simple in comparison with that of the female, though it is interesting to note that the male is almost equally degenerate. Hérouard (1906) has described the external features of the male of *Philichthys*

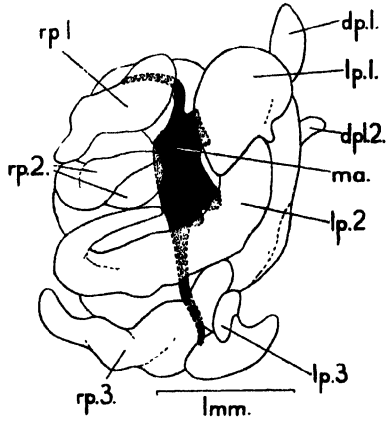

FIG. 6.—Ventral view of non-ovigerous female, showing position of male within the ventral groove. From a reconstruction.

Lettering as before.

amphiurae, and his figures show that the external form is very similar to that of the male of *Ophioica asymmetrica.* Stephensen (1935) suggested that the parasite described by Hérouard should be placed within the genus *Ophioica,* and this similarity in form of the males would support this suggestion further.

Fig. 7 shows the external features and fig. 8 a diagrammatic reconstruction of the principal internal organs of the male. From these figures it may be seen that the male is an elongated form, bearing anteriorly a pair of small papillae and more laterally a pair of elongated processes. The latter superficially resemble antennae, but a closer examination shows that they are simply lateral processes of the body-wall and are thus similar to the processes arising from the body of the female. The abdomen is elongated, tapers slightly

posteriorly, and is slightly forked at its extreme tip. Hérouard (1906) described the occurrence of genital papillae on the sides of the abdomen in the male of *Philichthys amphiurae*, but there is no sign of such papillae in the present instance. Moreover, it is likely that the genital pore or pores are terminal.

The internal organs consist of gut and the testes and their ducts (fig. 8).

The gut of the male is very similar to that of the female. The fore-gut may similarly be divided into ventral (chitin-lined) and dorsal (epithelial) parts, but the mid-gut is unbranched. The latter extends back into the abdomen, where it ends blindly (fig. 8, *g.*). Again, the hind-gut cannot be distinguished from the mid-gut. The mouth is not quite terminal (fig. 8, *m.*). Debris (apparently similar in nature to that seen in the mid-gut of the female) occurred in the mid-gut region.

The testes are paired. Each is a rounded sac, lying at the side of the anterior part of the gut (fig. 8, *te.*), but the two testes are connected by a bridge passing

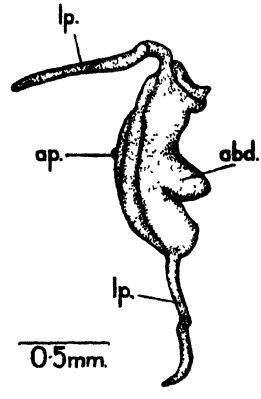

FIG. 7.—Postero-dorsal view of male. From a reconstruction.
abd., abdomen ; *a.p.*, anterior papilla ; *l.p.*, lateral process.

dorsal to the gut, slightly in front of the mouth (fig. 8, *te, b.*). The vasa deferentia arise on the outer side of each testis. They each run outwards into the lateral processes, then loop sharply back, running in towards the gut, finally turning sharply to run posteriorly down the abdomen, one on each side of the gut. Each vas deferens runs downwards to the extreme tip of the abdomen, and just posterior to the termination of the gut each bears a sac-like enlargement (fig. 8, *s.v.d.*). Posterior to these sacs the vasa deferentia end blindly.

At the junction of the vas deferens and testis, free spermatozoa can be seen lying massed together in the lumen of the former, but as they pass along the vas deferens, the spermatozoa become formed into spermatophores. The

staining reactions of the spermatophore sheath indicate that it is cuticular in nature. Thus the spermatophores of this parasite agree in the nature of their sheath with those of other Copepoda (Calman, 1909, p. 87). Within the posterior sac-like enlargement each spermatophore becomes considerably swollen and the outer part has a tendency to stain in Aniline-Blue. It is therefore probable that these sac-like enlargements secrete the cementing substance by means of which the spermatophores are attached to the female (Calman, 1909, p. 87).

As the course of each vas deferens is sinuous (cf. figs. 5, 8), it is difficult to obtain an accurate idea of the size of the spermatophores. In form they are

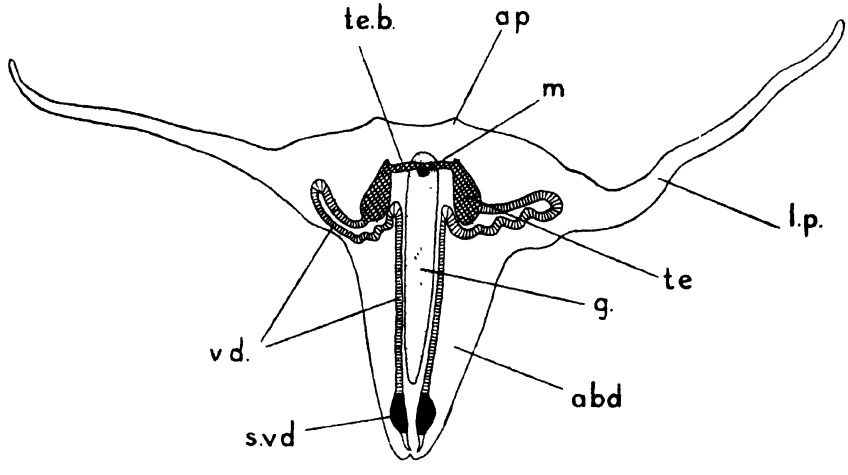

FIG. 8.—Diagrammatic dorsal view of male, showing the arrangement of the internal organs. (The abdomen is drawn as if pulled back.)

abd., abdomen ; *g.*, gut ; *m.*, mouth ; *s.v.d.*, sac-like part of vas deferens ; *te.*, testis ; *te.b.*, testis bridge ; *v.d.*, vas deferens. Other lettering as before.

cylindrical, one portion measured approximately 0·12 mm. in length and was 0·01 mm. broad at its broadest point. Their ends are rounded and the surface is raised into a series of small rounded papillae.

The absence of a genital pore raises the question of the mode of liberation of the spermatophores. There would seem to be three possibilities :—

(*a*) That the genital pore is minute and thus has not been detected in serial section—that is, it is less than 10 μ in diameter.

(*b*) That there is no genital pore, the spermatophores bursting their way out of the tip of the abdomen.

(*c*) That the genital pores are formed when the spermatophores are ready to be liberated.

The first possibility does not seem likely owing to the size of the spermatophores, especially after the addition of the cementing substance. With regard to the second possibility it was noticed that at the end of their course the spermatophores on each side had been displaced laterally through the abdomen and were lying outside the latter. In this case the tearing was most probably due to faulty sectioning, but the possibility that liberation in this way is the normal method in life cannot entirely be dismissed, as the wall of the vas deferens and the integument of the abdomen are both very delicate at this point.

The possibility that the genital pores were not yet open seems the most likely, as there is other evidence which would support this suggestion. From a comparative study of the genital ducts of the non-ovigerous and ovigerous

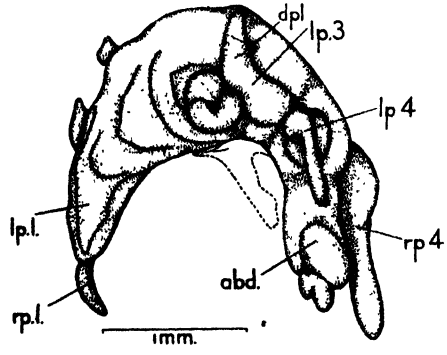

Fig. 9.—Lateral view (from left-hand side) of ovigerous female. From a reconstruction.

abd., abdomen; *dpl.*, left dorso-lateral process; *lp.* 1–4., left ventro-lateral process 1–4; *rp.* 1, *rp.* 4, right ventro-lateral process 1, right ventro-lateral process 4. The dotted outline indicates the position of the male.

females it can be seen that growth of the glandular part of the oviduct may not be complete until after large numbers of ova have accumulated in the more dorsal parts of the reproductive system, since in the non-ovigerous female there was only one such glandular duct and that ended blindly, whereas in the ovigerous individual there were two ducts present and they appeared to open at the tip of the abdomen. Further, attached to the ovigerous female was a male (fig. 9). The internal organs of this male had practically disappeared and the chitinous exoskeleton was much crumpled in consequence, but there were openings at the posterior end of the abdomen which were probably the genital pores. These observations suggest that the genital openings in both sexes may not be perforated until the genital products are ready to pass out through them.

SPECIMEN 2.

This also comprised a female with an attached male.

(a) *The ovigerous female.*

The ground-plan of the anatomy of this form is essentially the same as that of the non-ovigerous female, but the extrusion of the egg-masses and the development of more processes from the body make its general appearance so unlike that of the non-ovigerous female that a separate description is necessary.

(i) *External features.*

These are shown in figs. 9 (from the left-hand side) and 10 (from the right-hand side).

When the egg-masses pass out of the oviducts they become massed under the ventral surface of the female and are embedded in the investing Ophiuroid

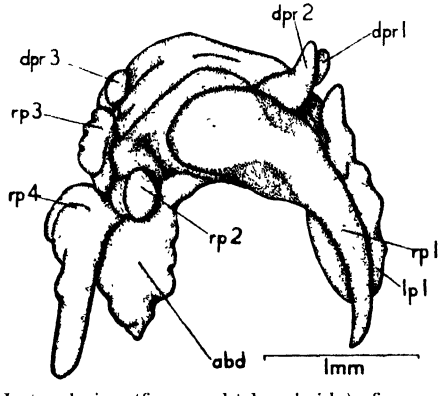

FIG. 10.—Lateral view (from right-hand side) of ovigerous female. From a reconstruction.
dpr. 1–3, right dorso-lateral process 1–3 ; *r.p.* 1–4, right ventro-lateral process 1–4. Other lettering as before.

tissue. Thus they are enclosed in what has been termed a 'brood-pouch' (Stephensen, 1935). Stephensen (loc. cit.) was unable to determine whether the membranous wall of this pouch was formed by the host or by the parasite, but in the present case it is quite clearly formed of host-tissue (fig. 12, *br.p.*). The presence of this brood-pouch ventrally makes the whole organism more globular in appearance and in particular presses the ventro-lateral processes apart, so that they no longer close over the ventral groove, but appear laterally (figs. 9, 10, *lp.* 1–4 ; *rp.* 1–4).

On the left-hand side four processes can be distinguished, which project laterally and are each embedded in the host-tissue. The longer processes (or, more probably, those which are not contracted) project beyond this tissue and appear externally (see fig. 1, which was drawn from this specimen before

sectioning). The anterior process (fig. 9, *lp.* 1) projects more anteriorly than laterally, and there is a corresponding process on the right-hand side (fig. 9, *rp.l.*). As these processes appear to be pre-oral in position, it is possible that they may represent antennae. There is also a small process which arises more dorsally (fig. 9, *dpl.*).

The abdomen is clearly developed in this specimen (figs. 9, 10, *abd.*). It projects freely into the brood-pouch (fig. 12, *abd.*) and it is slightly forked at its tip.

On the right-hand side there are also four processes which project laterally (fig. 10, *rp.* 1–4), though these are not always placed symmetrically with respect to those of the other side. In this view it can also be seen that both the left and right anterior processes (fig. 10, *lp.* 1, *rp.* 1.) bear short lobe-like branches on their inner sides. Hérouard (1906) has recorded that the antennae of *Philichthys amphiurae* are forked. On this right-hand side it is also possible to distinguish three dorso-lateral processes (fig. 10, *dpr.* 1–3).

On the left-hand side the lateral wall of the body showed traces of segmentation, Four segments could be distinguished, as well as the abdomen. These traces of segmentation were not pronounced and were absent altogether on the right-hand side.

(ii) *Internal anatomy.*

As in the non-ovigerous female, the only internal organs are the gut and the reproductive organs.

The general anatomy of the gut is similar to that of the non-ovigerous female, but as the gut and its branches are much less compressed than in the latter (compare figs. 5 and 12) it was possible to investigate the detail of this branching of the mid-gut rather further in the present instance.

The anatomy of the fore-gut is precisely similar. The mid-gut branches penetrate into the proximal parts of the lateral processes and, correlated with the asymmetrical arrangement of the latter, they are also asymmetrical (fig. 11). Just anterior to the mouth is a dorsal diverticulum and it will be noted that the mouth itself is not in the mid-ventral line of the gut. The gut does not penetrate into the abdomen, but ends blindly at its base.

The general arrangement of the reproductive organs is similar to that of the non-ovigerous female. The ovaries are definitely paired and each communicates with a sac-like oviduct which ramifies round the gut, branches entering the lateral processes and the abdomen (fig. 12, *ovid.*). This branched part of the oviduct still contained some ova, although they were not so closely packed as in the oviduct of the ovigerous female. Within the ovary developing ova could still be seen, so that the production of fully formed eggs was apparently still going on. As before, the distinction between ovary and oviduct was scarcely perceptible (fig. 12, *ov.*, *ovid.*).

The branched oviduct on each side eventually leads into the glandular terminal part which lies within the abdomen (fig. 12, *gl.ovid.*). The two glandular

tubules run down through the abdomen and appear to open near the tip of the latter, the openings being directed towards its ventral side. Owing to the state of preservation of the material, it is difficult to be absolutely certain that the oviducts do open in the way just described, but there are strong indications that the interpretation that has been given is correct.

Stephensen (1933), in his description of *Ophioica ophiacanthae*, figures three pairs of ' oblong organs ' associated with the genital openings, and he suggested

FIG. 11.

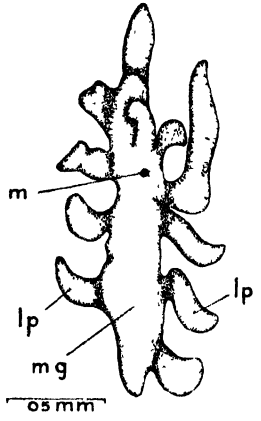

FIG. 12.

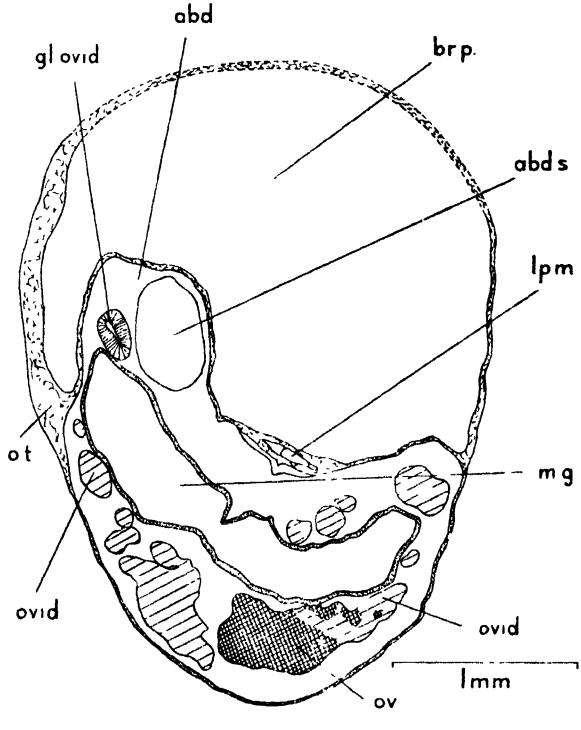

FIG. 11.—Gut of ovigerous female in dorsal view. From a reconstruction. *l.p.*, lateral process of mid-gut ; *m.*, position of mouth ; *m.g.*, mid-gut.

FIG. 12.—Vertical section of ovigerous female. *abd.s.*, abdominal sac (? spermatheca) ; *br.p.*, brood-pouch ; *gl.ovid.*, glandular part of oviduct ; *lp.m.*, lateral process of male ; *m.g.*, mid-gut ; *ov.*, ovary. Other lettering as before.

that these organs were ' sort of mucous glands for the eggs '. Later (1935), he found that the genital openings were probably at the tip of the abdomen and that therefore these ' oblong organs ' were not to be associated with the reproductive organs at all. He was unable to suggest what function they might serve. These organs (as is clear from his figures, e.g. Stephensen (1935), p. 14, fig. 8) are not contained within the abdomen, but within processes of the

body-wall. It is possible to suggest an explanation for Stephensen's figures on the basis of the present material. In *Ophioica ophiacanthae* he describes three processes, each containing a pair of ' oblong organs ' ; in *O. appendiculata* he figures two such processes, again each containing a pair of these organs. In both cases he only examined his specimens externally and in both cases he did not record the presence of attached males. It thus seems possible that the structures that he has described as processes of the female (which contain these ' oblong organs ') are really attached males, especially as Hérouard (1906) has recorded that four males may be found attached to a single female of *Philichthys amphiurae*. This suggestion (admittedly tentative) is supported by the fact that the point of ' attachment ' of these processes is on the ventral surface of the female—that is, at precisely the point of attachment of the male in *Ophioica asymmetrica* (figs. 6, 9). As both male and female are encased in host-tissue and as the male is closely pressed against the ventral surface of the female, it would be difficult, upon an examination of external features only, to discover that two sexes were present.

Contained within the ventral part of the abdomen is an elongated thin-walled sac (fig. 12, *abd.s.*). This sac is not connected with any of the internal organs and no opening can be traced from it to the exterior. There is no trace of this sac in the non-ovigerous female, but in the ovigerous female it is quite definitely an organ of some sort, though, because of its lack of communication either with the exterior or with any of the internal organs and the absence of contents, it is not possible to make more than tentative suggestions as to its identity. It is not to be connected with the gut, so that it may possibly be part of the reproductive system. If this deduction is correct, then this sac may be the spermatheca. Possibly a more detailed examination of more freshly preserved material would make its identity clearer.

Eight egg-masses were present which had, presumably, all come from the brood-pouch of the ovigerous female. Stephensen (1935) records a maximum of six egg-masses associated with a single female of *Ophioica appendiculata*. In the present species, each egg-mass is an ovoidal body, one specimen measuring 1·5 mm. along the major axis, 0·9 mm. along the minor. Thus there appears to be a size difference in the egg-masses of the three species of *Ophioica* that have been described, namely :—

Species.	Major axis. (mm.).	Minor axis. (mm.).
O. asymmetrica	1·5	0·9
O. appendiculata.....	1·0	0·6
O. ophiacanthae	0·5	0·3

(The measurements for the last two species are taken from Stephensen, 1933 ; 1935.)

All the eight egg-masses were examined, but each consisted of a mass of yolky ova, cemented together. Stephensen (1935) found that in some of the

eggs of the egg-masses of *Ophioica appendiculata*, development had proceeded as far as the nauplius stage and thus concluded that the various egg-masses differed in age.

(b) *The male.*

The position of attachment of the male is shown in fig. 9. The orientation of this sex with regard to the female is the same as in the specimen described above, but, owing to the development of the brood-pouch ventrally in the present instance, the male projects into this pouch, instead of being enclosed within the processes of the female.

The external features of the male are similar to those of the male described earlier, but the whole body had shrunk considerably (as evinced by the crumpling of the exo-skeleton), presumably owing to the degeneration of the internal organs. The latter had practically disappeared; the gut had disappeared except for a small sac anteriorly; there was no sign of gonad, and the vasa deferentia, though clearly visible, were degenerating. As has been mentioned previously, there was evidence of genital pores at the apex of the abdomen, though, owing to the degeneration of the more anterior parts of the vasa deferentia, it was difficult to trace direct connections between these pores and the rest of the reproductive system.

Discussion.

This study of the anatomy of *Ophioica asymmetrica* has added fresh details to what is known of the structure of this aberrant genus, notably a more precise knowledge of the internal anatomy and the demonstration of the presence of the male, found closely applied to the ventral surface of the female. At the same time other problems are raised.

Stephensen (1933, 1935) was not able to detect the presence of an alimentary canal in the species he described and therefore came to the conclusion that the food was absorbed from the host through the serpentine processes. Hérouard (1906) thought that the second antennae of *Philichthys amphiurae* played a similar part in the nutrition of this species. The presence of a well-developed gut in the present series of specimens thus raises the question as to how far these parasites do feed on particulate food. In the non-ovigerous female and its attached male and again in the ovigerous female, debris could be seen in the mid-gut and in the first specimen there were also large food-masses. This would suggest that food-particles are being taken in through the mouth and digested in the mid-gut. On the other hand, it is not easy to see how this food reaches the mouth, since the whole animal is enclosed within the tissues of the host. It is not likely that pieces of Ophiuroid tissue are ingested, since there is no evidence that pieces of this tissue are being broken away near the mouth, nor do the food-masses within the gut resemble the Ophiuroid tissue without.

Yet there is no positive evidence against the theory that food may be absorbed all over the surface of the body and particularly by the body-processes. Yonge (1932) has pointed out that of the cuticular and chitinous layers which go to form the integument of Decapod Crustacea, the cuticular layer is impermeable, whereas the chitinous layer is permeable, and considers that the cuticle is of fundamental importance in controlling the permeability of the integument of all Crustacea. In this connection it is interesting to note that this outer cuticular layer is practically absent in *Ophioica asymmetrica*, as it is only to be found along the sides of the left ventro-lateral process of the non-ovigerous female (fig. 2, *lp*. 2). Thus it would appear that there is no impermeable barrier to the inward diffusion of food from the host-tissue. Possibly a comparison may made between *Ophioica asymmetrica* and the Ascothoracican Cirripede, *Baccalaureus maldivensis*, since the latter is also enclosed within a mass of host-tissue, lacks cuticle over much of the surface of the body, and has a much branched mid-gut and where it is suspected that food may be absorbed from the enclosing host-tissue (Pyefinch, 1936). But if this method of food-absorption is the one which takes place in *Ophioica*, it would be expected that there should be some evidence of such absorption, evidence such as occurs, for instance, in the Ascothoracican *Baccalaureus torrensis* (Pyefinch, 1937). Careful examination of the tissues and the gut-contents of this Copepod yield, however, no such evidence and it is this fact, together with the presence of debris in the gut, that suggests that actually solid food may be taken into the gut and digested in the normal way.

There are also points of interest in the processes of reproduction. It is not clear, from a study of the material available, how the spermatophores leave the male, how they are transferred to the female, whether, after transference, they are stored within a spermatheca, and where fertilisation takes place. So far as the evidence of the stage of development of the egg-masses goes, it seems likely that all the eggs are produced at about the same time. Further, it may also be concluded that the period of egg-production exceeds that when there are spermatophores available to fertilise the eggs produced, since in the ovigerous female the ovaries were still full of ova, but there was no evidence of the presence of spermatophores, and, since the internal organs of the male had practically disappeared, no further spermatophores could be produced. Possibly in those cases where several males are attached to one female (*Philichthys amphiurae* and possibly *Ophioica ophiacanthae* and *O. appendiculata*) the former may come to maturity successively and thus extend the period during which fertile eggs may be produced.

It will be clear from the foregoing discussion that access to more material, either living or freshly fixed by careful methods, would go far towards solving some of these problems. In view of the specialised nature of this parasite an investigation of this sort would seem desirable. Further, if the form described as *Philichthys amphiurae* (Hérouard, 1906) is really a species of *Ophioica*, such a supply should not be difficult to obtain, since its host, *Amphipolis*

(*Amphiura*) *squamata* is recorded as being common round the coasts of this country (Mortensen, 1927, p. 222 ; Plymouth Marine Fauna, 1931, p. 295).

Systematic position.

Stephensen (1933) formulated the definition of *Ophioica ophiacanthae* as follows :—

' Endoparasitic Copepods in Ophiurids. The body of the adult female more or less unsymmetrical, with long serpentine appendages and several (4 ?) genital openings, and more than 2 (viz. 4) egg-masses. Probably there are no inner organs other than the ovary.'

In his later description of *O. appendiculata* (1935) he modified this definition only slightly, pointing out that the genital openings were organs of unknown function and ' that there may be up to 6 egg-masses '.

It is not easy to make this definition of *O. asymmetrica* more precise, because of the variation in the form of the body of the adult female. This variation in form appears to arise from two causes :—

(*a*) As the female grows older, that is, in the development from the non-ovigerous to the ovigerous stage, further lateral or ventro-lateral processes may appear.

(*b*) The asymmetry of the body, due to compression within the bursa of the host Ophiuroid. This is especially seen in the asymmetry of the dorso-lateral processes (figs. 4, 9, 10). The asymmetry of these processes in the present material may indicate that there is no precise orientation of the parasite within the bursa of the host, since in the non-ovigerous female the dorso-lateral processes are best developed on the left-hand side of the body and on the right-hand side in the ovigerous female.

An outline definition of *Ophioica asymmetrica* may, however, be framed as follows :—

Copepods endoparasitic in *Ophiacantha imago* (Lyman), totally enclosed within the tissues of the host. Adult female with a variable number of paired serpentine processes. Dorso-lateral processes, asymmetrically arranged, may also be present. Internal organs consisting of gut and reproductive organs only. Eight egg-masses may be present.

Adult male enclosed within the ventral groove of the female and closely applied to the surface of the latter. Body unsegmented and with a pair of elongated lateral processes. Internal organs, gut, and reproductive organs only.

Thus in the present state of knowledge of this aberrant genus, it is really only possible to characterise species by their distribution in different hosts. One additional specific distinction has already been noticed, the difference in size of the egg-masses, though this is not a very suitable character.

While it is thus difficult to frame adequate definitions distinguishing one species of *Ophioica* from another, it is even more difficult to envisage the

relationships of this genus with the rest of the Eucopepoda. The solution of this problem must depend upon a knowledge of the life-history of *Ophioica*.

The specimens and sections upon which this description is based have been deposited at the British Museum (Natural History).

In conclusion, I must thank Dr. I. Gordon for the opportunity of examining this material and Dr. W. T. Calman, Mr. D. D. John, and Dr. I. Gordon for their help and advice in the earlier stages of this investigation.

Summary.

1. An account is given of the external and internal anatomy of a new species of the aberrant Copepod genus, *Ophioica*, occurring within the Ophiuroid, *Ophiacantha imago* (Lyman).

2. Specimens of ovigerous and non-ovigerous females, with their attached males, were examined.

3. The body of the adult female is unsegmented and possesses several pairs of serpentine processes. Three such pairs are present in the non-ovigerous female and four pairs in the ovigerous female. There are also processes which arise dorso-laterally. The abdomen is distinct only in the ovigerous female.

4. The internal organs of the female are gut and reproductive organs. The former can be divided into fore- and mid-gut, the latter much branched. If a hind-gut is present it cannot be differentiated from the mid-gut. In the ovigerous female the ovaries are paired and the genital openings are probably at the tip of the abdomen.

5. The male is attached to the ventral side of the female, but only the male attached to the non-ovigerous female was fully developed. It is also unsegmented, with a tapering abdomen and a pair of serpentine lateral processes. The internal organs are again gut and reproductive organs only and the genital openings appear to be at the tip of the abdomen. In the male attached to the ovigerous female the internal organs had practically disappeared.

6. It was not possible to determine the process of transference of the spermatophores from the male to the female. It is probable that the genital openings are only perforated at maturity in both sexes.

7. The ovigerous female carried eight egg-masses, pressed under the ventral surface of the body and enclosed within a ' brood-pouch ' of host-tissue.

8. Certain points in the biology of these parasites, consequent upon their enclosure within the tissues of their host, are discussed.

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Some Nemerteans from South Africa and a note on *Lineus corrugatus* M'Intosh.

By J. F. G. WHEELER, D.Sc., F.L.S., Bermuda Biological Station for Research.

(With 13 Text-figures)

[Read 11 April 1940]

IN the course of Professor T. A. Stephenson's ecological survey of the coast of South Africa a number of Nemerteans were collected and sent to me for examination. There were in all twenty-two specimens, taken from various localities on the coast from Oudekraal, south of Table Bay, on the west, to Bats Cave Rocks, about two miles north-east of East London, on the east. I was interested to note that *Lineus corrugatus* M'Intosh had been discovered here, since this form is characteristically antarctic. I found, however, that a close external similarity of the specimens to *L. corrugatus* obscured very definite differences. *L. corrugatus* must accordingly be deleted from the Nemerteans recorded from South Africa up to the present.

As the survey is specifically concerned with the rocky parts of the coast, I am surprised at the absence of *Tubulanus nothus* Bürger, which was one of the commonest forms found at Saldanha Bay, further to the westward, where it forms conspicuous tangles among the holdfasts of the large seaweeds. Four species only of the twelve here recorded were found at Saldanha Bay, namely, *Emplectonema ophiocephalum*, *Zygonemertes capensis*, *Lineus ruber*, and *Cerebratulus fuscus*. *Lineus olivaceus*, described by Stimpson from Simon's Bay in 1856 and previously synonymized with *L. ruber*, has been re-established.

Taking the localities from west to east the recorded species are as follows :—

Survey reference.	Locality and species found.	Reference to specimens and slides.	Number of specimens.
	Oudekraal, south of Sea Point, south of Table Bay.		
A.395	*Paradrepanophorus stephensoni*, sp. n.	SAN 2	1
A.101	,, ,, ,, ...	SAN 12	1
A.339	*Emplectonema ophiocephalum* (Schmarda)	SAN 13	1
A.174*a*	*Zygonemertes capensis* Wheeler	SAN 14	1
A.245	*Cerebratulus fuscus* M'Intosh	SAN 7	2
	False Bay, St. James.		
F.284	*Lineus ruber* (O. F. Müller)	SAN 3	1
F.283	,, ,, ,, ...	SAN 9	1
F.282	*Lineus lacticapitatus*, sp. n.	SAN 5	1
F.216	*Cerebratulus fuscus* M'Intosh	SAN 1	1

Survey reference.	Locality and species found.	Reference to specimens and slides.	Number of specimens.
	Roof Bay, Port Elizabeth.		
E.27	*Lineus ornatus*, sp. n.	SAN 4	4
E.28	*Lineus capensis*, sp. n.	SAN 6	1
	Shelly Beach, East London.		
L 108	*Amphiporus africanus*, sp. n.	SAN 11	1
L.343	,, ,, ,,	SAN 18	1
L.414	*Zygonemertes capensis* Wheeler	SAN 17	1
L.35	*Lineus olivaceus* (Stimpson)	SAN 10	2
L.340	,, ,, ,,	SAN 15	1
	Bats Cave Rocks, East London.		
L.512	*Prostoma dutoiti*, sp. n.	SAN 16	1
L.35	*Lineus olivaceus* (Stimpson)	SAN 10	—

In November 1938 and April 1939 more Nemerteans collected during the survey were sent to me. These have been identified as follows :—

Port Nolloth (Sept. 1938).

NN45	*Zygonemertes capensis* (green var.)	SAN 25 *a*.
	Zygonemertes capensis (brown var.)	SAN 25 *b* (immat. male).
	Emplectonema ophiocephala	SAN 25 *c* (post. end only).

Lambert's Bay (July and Aug. 1938).

B.64	*Lineus ornatus*	SAN 20 (ripe female).
B.202	*Zygonemertes capensis*	SAN 21.
B.201	*Lineus olivaceus*	SAN 22.
B.143	*Cerebratulus aerugatus* Burger	SAN 23 (5 heads, 7 pieces of body, 1 tail).
B.203	*Zygonemertes capensis*	SAN 24 (3 specimens)
B.63	*Prostoma candidum* (O. F. Muller)	SAN 26.

Shelly Bay, East London (July 1937).

L.407	*Prostoma dutoiti*	SAN 29.
L.414	*Amphiporus africanus*	SAN 28.

Bats Cave Rocks, East London (July 1937).

L.332	*Amphiporus* sp. (too much distorted for identification).	SAN 27.

Port Nolloth is about three hundred miles from Cape Town on the west Coast. The sequence of localities from west to east should be :—Port Nolloth, Lambert's Bay, Oudekraal, St. James, Port Elizabeth, and East London.

I wish to thank Professor Stephenson for allowing me to examine this material, and also Miss Joyce Eyre, who sent further specimens from the survey collections.

Description of the species.

Order HETERONEMERTEA.

Genus LINEUS Sowerby.

LINEUS CAPENSIS, sp. n. (SAN 6).

A single specimen (E.28), noted as 'brown, very long, under stone in channel' was collected at Reef Bay, Port Elizabeth, on July 5, 1936.

In spirit the body is knotted together (fig. 1, A). The approximate length is 24·0 cm., the greatest breadth 6 mm., and the thickness 3 mm. The body is flattened and ribbon-like, except at the head, and has a shallow longitudinal mid-dorsal ridge or hump. Transverse contraction wrinkles are present and longitudinal wrinkles occur, especially behind the head. The thin white proboscis is everted (8·5 cm.). The head is slightly flattened. The cephalic slits are thin and their ends are not sharply defined. Their length is 3 mm., including a shallow groove extending a short way beyond their posterior limit. The mouth is just behind the level of the posterior ends of the slits. It is a small slit with inturned lips, not pursed or swollen, and is of the same colour as the rest of the head. The tail ends bluntly and has no appendage. In colour the body is pale brown with no trace of markings, darker dorsally on the head, the deeper colour ending at the slits. No eyes are visible, nor do any become apparent in cedar oil. The proboscis-pore is just ventral to the tip of the snout. Distortion of the head has taken place, seen in the serial sections as a right-angle twist upwards at the proboscis pore and another right-angle turn immediately behind this point.

No frontal organs are present. The tip of the head has vertical and horizontal furrows and a mid-dorsal longitudinal deep furrow that can be traced on the body. The cephalic slits are deep, and the scattered head-glands stain deeply with hæmatoxylin (fig. 1, B). At the anterior end of the mouth the dorsal body-wall consists of an epithelium of tall cells, 0·05 mm. thick, appearing red from the large number of eosinophile bodies present in it. The cutis-layer contains approximately equal numbers of hæmatoxylin- and eosin-stained glands and is 0·125 mm. thick. The eosinophile glands traverse a space about equal to the epithelium in thickness between the glandular layer and epithelium. There is no clear layer of the cutis beneath the glandular layer (fig. 1, C). The ventral epithelium is thinner than the dorsal.

The anatomy is typically heteronemertean, but certain characters appear in this species that are not present in the others to be described, which may render identification possible from preserved material. In the posterior third of the body the muscle-layers are reduced, so that dorsally they appear thinner than the epithelium and cutis. The lateral nerves are well below the margins of the body (fig. 1, E). The proboscis possesses a very well-marked longitudinal glandular tract, the central portion of which stains deeply with

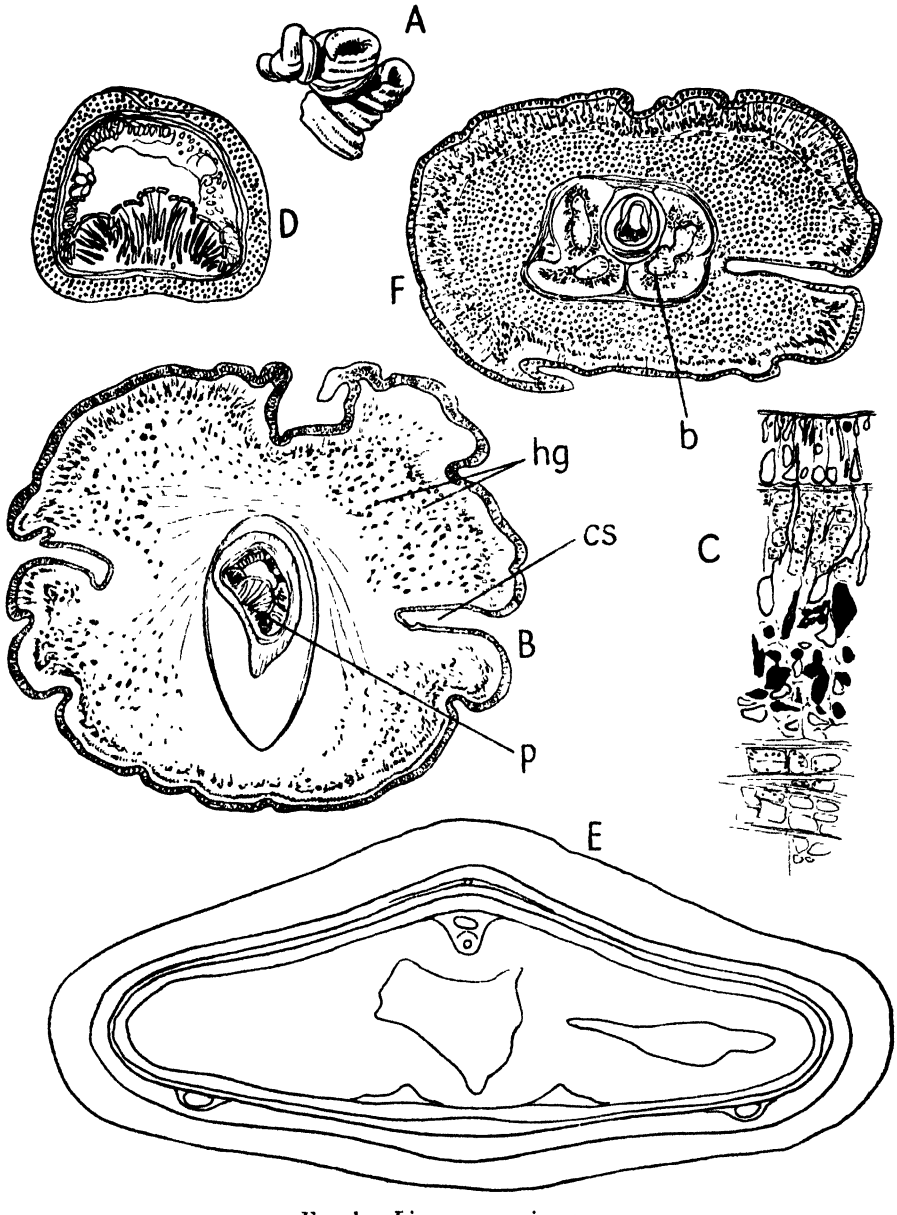

FIG. 1.—*Lineus capensis*, sp. n.

A. Sketch of spirit-specimen, × 1. B. Transverse section through anterior end of head, showing head-glands (*hg*), cephalic slits (*cs.*), and proboscis (*p*). C. Dorsal body-wall in region of anterior end of mouth; haematoxylin staining in black, eosin staining left blank. D. Section of proboscis. E. Diagram showing section of posterior third of body. F. Transverse section through brain (*b*).

eosin, while a smaller lateral tract on each side stains deeply with hæmatoxylin (fig. 1, D). The mass of unstained cells that occur close to the cephalic slits in *L. lacticapitatus* is not present. The brain is not very large for the size of the head (fig. 1, F) and no neurochord cells are present.

LINEUS LACTICAPITATUS, sp. n. (SAN 5).

A single specimen (F.282) was collected from St. James, False Bay, on August 3, 1936. It was noted as ' fairly common buried in sand under stones in middle shore '. In life it was ' large, mauvish grey with white tip at head end '.

The preserved specimen is 2·6 cm. long and 4·6 mm. wide. The body tapers and is flattened dorso-ventrally. The greatest diameter is about 1 cm. behind the head. The tail is acutely pointed ; the head blunt. There is no caudal appendage and the body is transversely wrinkled only. In colour it is blackish grey, anteriorly uniform, posteriorly lighter beneath. The tip of the head is uncoloured dorsally and ventrally for a distance of 1·5 mm. and the pigmented part then starts abruptly. The cephalic slits are straight, 3·5 mm. long, and the mouth, a 2-mm. slit without protruding lips, commences at the level of the ends of the slits. No eye-spots are visible, nor were they afterwards seen in cedar oil or in sections.

The characteristic feature of this Lineid is found in the head, where on each side of the cephalic slits a conspicuous mass of unstained cells occurs (fig. 2, A, B).

Frontal organs are present. The head-glands are thin and diffuse. They stain lightly with hæmatoxylin and reach back to the brain. The epithelium is thin (0·045 mm. dorsally in the brain region) and contains large eosinophile bodies, thus appearing red in sections. The cutis is deep, though not as deep as in *L. capensis*, hæmatoxylin-stained glands are few and the eosinophile glands are fewer still and occur at a deeper level (fig. 2, C). The proboscis is thin. It does not possess the glandular tracts so distinctive of *L. capensis*.

The cephalic slits are wide and rather shallow. The brain is larger than that of *L. capensis*, but similar in structure. No neurochord cells could be distinguished (fig. 2, A, D). A section through the body in the posterior third region indicates that the muscle-layers are very much thicker than the epithelium and cutis, that dorsally the outer longitudinal muscles are far thicker than they are ventrally, and that the lateral nerves pass down the body at its extreme margins, so that owing to the convexity of the ventral surface in this specimen they appear above the horizontal plane of greatest width (fig. 2, E).

The unpigmented tip of the head, which must be conspicuous in the living animal, recalls *Cerebratulus aerugatus* Bürger, of which an anterior end was found at Saldanha Bay. Dr. Baylis, of the British Museum (Natural History), kindly undertook to check the absence of unstained glandular masses and the presence of neurochord cells in the sections of this species deposited at the Museum. His confirmation has established the essential difference between these externally similar forms.

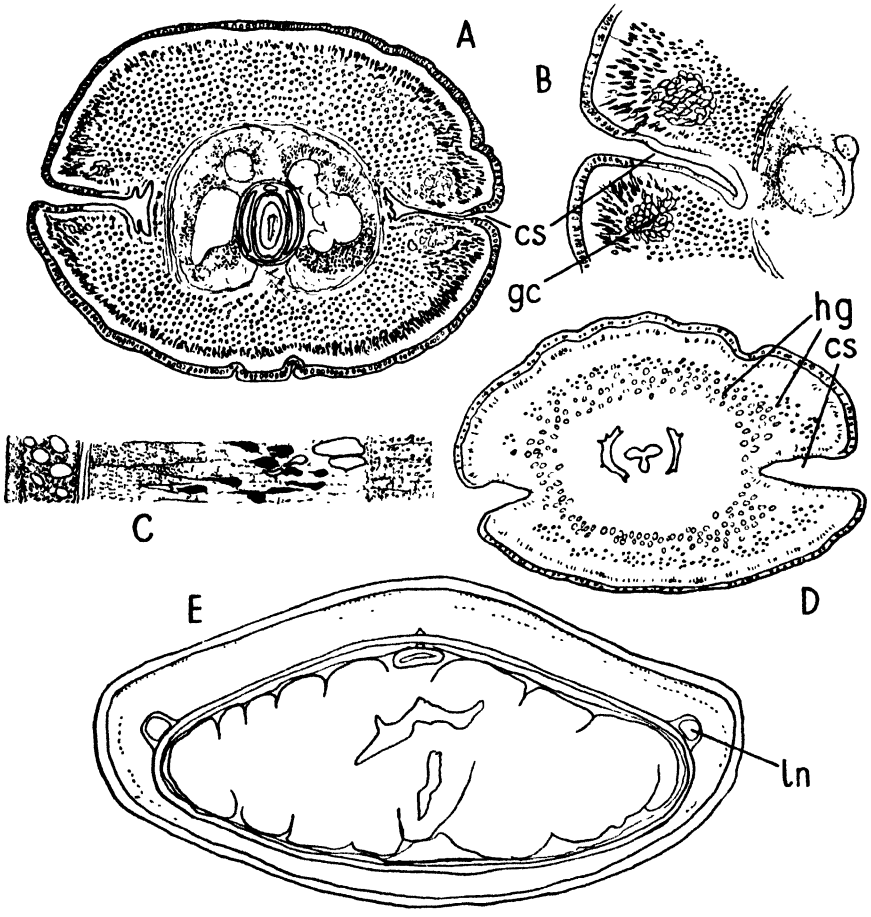

FIG. 2.—*Lineus lacticapitatus*, sp. n.

A. Section through brain. B. Enlarged section through cephalic slit, to show unstained masses of cells (*gc*). C. Section through dorsal body-wall at anterior end of mouth; haematoxylin staining in black, eosin staining left blank. D. Section through anterior end of head, to show head-glands (*hg*) and cephalic slits (*cs*). E. Hand-section through posterior third of body, to show position of lateral nerves (*ln*).

LINEUS OLIVACEUS (Stimpson) (SAN 10 & 15).

Three specimens of this species were included in the collection. One of these, under the reference L.35, was collected at Shelly Beach, East London, on July 6, 1937; another at Bats Cave Rocks, East London; a third (L.340) was also taken at Shelly Beach, no date being given. Notes made on the living specimens are 'L.35, a fairly long cylindrical worm, dark purplish grey in colour, living between the cement-like tubes in a colony of the tubicolous Polychaet *Pomatoleios crosslandii*. Bats Cave Rocks: Embedded in lumps

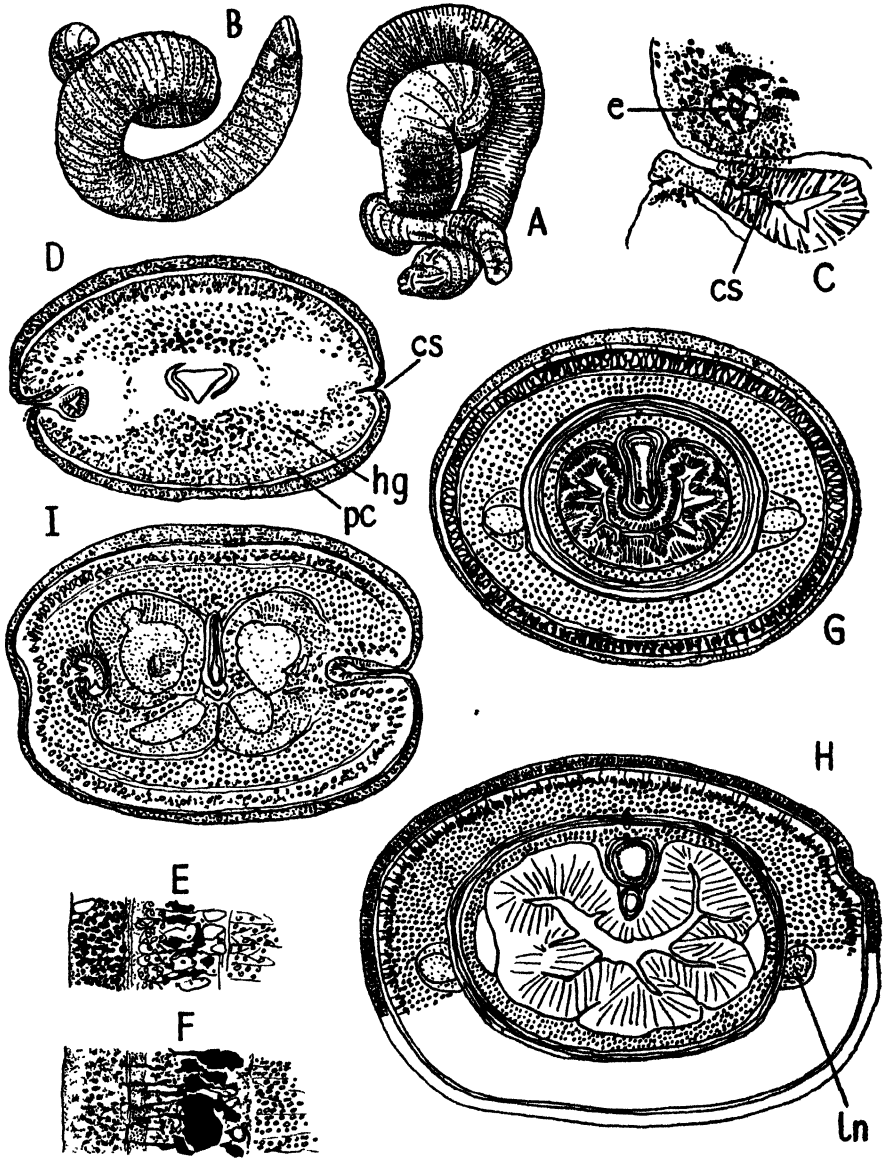

FIG. 3.—*Lineus olivaceus* (Stimpson).

A, B. Specimens in spirit, SAN 10 *a* & *b*; C. Transverse section through cephalic slit (*cs*), to show eye-spot (*e*). D. Transverse section through anterior end of head, to show head-glands (*hg*), cephalic slits (*cs*) and pigment in the cutis (*pc*). E, F. Dorsal body-layers at the posterior end of the mouth, with round haematoxylin-stained bodies in the epithelium, for comparison with fig. 5, B, C. G. Transverse section of body behind the brain. H. Transverse section of the body near the tail (SAN 10 *b*). I. Transverse section through brain.

of compound ascidians and sponges on the wall of a pool low down on the shore'. L.340: 'Black in colour. Only one found between the "roots" of *Ecklonia radiata* in a fairly deep channel in the middle of the shore.'

In spirit two of the specimens (SAN 10 *a* & *b*) are blackish blue-grey, and almost exactly similar in size and shape, 2·0 cm. long and 2·0 mm. in diameter. SAN 15 is olive-green in colour, paler beneath in patches, 5·1 cm. long, 1·3 mm. broad at the broadest part of the head, and just under 1 mm. thick (fig. 3, A, B). In all the specimens the cephalic slits and the mouth are pallid. The head is somewhat flattened and obtusely pointed in outline from above. Transverse contraction wrinkles mark the surface of the body, and a deeper furrow occurs between the posterior ends of the cephalic slits and the anterior end of the mouth. The body tapers towards the tail, but the tail itself is bluntly pointed. There is no caudal appendage. No eyes can be distinguished. All three worms were curiously hard to the touch and were unusually brittle to handle, almost as though they had at some time dried up. This was also suggested by the chalky appearance of the body when broken. The worms sectioned perfectly, however, so that these peculiarities appear to be characteristic of the species. One specimen (SAN 10 *a*) was cleared in anilin oil. No eyes could be discerned, but the pigment, which appears olive-green and extends to the sides of the head, is densely accumulated in the cutis-layer, obscuring the eyes which were found later in the sections. They are small and few—less than six on each side above the cephalic slits (fig. 3, C).

Frontal organs are present, and diffuse head-glands staining deeply with haematoxylin (fig. 3, D).

In the region of the mouth the epithelium (0·045–0·06 mm. thick) appears blue. This is due to the presence of many small haematoxylin-stained round bodies with few large eosinophile masses. The cutis-glands differ, being in SAN 10 conspicuously blue from deeply stained large glands and few eosinophile glands, while in SAN 15 eosinophile glands preponderate. These differences are possibly due to the recent activities of the glands (fig. 3, E, F).

The gut is regular and the lateral nerves course down the body slightly below the horizontal plane at the widest part of the body (fig. 3, G, H). A single excretory duct was observed passing out laterally above the nerve on each side just over 1 mm. behind the posterior end of the mouth.

The brain is large, larger relatively to the size of the head than in *L. capensis* or *L. lacticapitatus* (fig. 3, I). The cephalic slits are not very deep, and the unstained cells of *L. lacticapitatus* are absent. No neurochord cells can be observed.

In 1856 Stimpson described, under the name *Meckelia olivacea*, a worm from Simon's Bay: 'Slender, convex above especially anteriorly where is also the greatest breadth. Head with a longitudinal slit which extends far down each side and is covered by a slight vertical notch at the anterior extremity. Genital opening large on the lower surface of the neck just behind the termination of the lateral slit. Colour anteriorly very dark greenish or olivaceous;

posteriorly a much paler green. Length 3 inches, width 0·1 inch '. In Stimpson's second paper (1857) this becomes *Cerebratulus oleaginus*. Bürger (1895) synonymised *M. olivacea* with *Lineus gesserensis*, i.e. *L. ruber* (O. F. M.). M'Intosh had previously synonymised the later name in the same way. M'Intosh (1873) says of *L. gesserensis* : ' Two very distinct hues are characteristic of this species, viz. reddish-brown and dull olive, while pale reddish and green varieties are also occasionally met with. The pigment is generally darkest in front, before and behind the reddish mark in the ganglionic region, the rest of the body being uniformly tinted except towards the tail which is paler. The snout is surrounded by a broad pale region, as far back as the termination of the fissures. The mouth is surrounded by a pale margin '.

Stimpson's description, so far as it goes, applies quite well to the form described here, although ' genital opening large ' does not appear to correspond with the small mouth. Apart from the fact that the size of the mouth is usually variable, as a genital opening the aperture is undoubtedly large. Superficially *L. olivacea* corresponds with the green form of *L. ruber*, but I have come to the conclusion that its inclusion is inadmissible. Not only is there a colour difference in life but the preserved forms are distinct in colour and in the curious brittleness of the body which is accompanied by a chalky whiteness of the broken surfaces. Further, the epithelium in sections of *L. olivacea*, stained with hæmatoxylin-eosin, can readily be distinguished from those of *L. ruber*. Both series of *L. olivacea* show an epithelium laden with granules deeply stained with haematoxylin, so that the general effect is blue, while in both series of *L. ruber* (SAN 3 & 9) it is brilliant with eosin-stained masses (the Flaschendrüsenzelle of Bürger). It is possible that this distinction is accidental, that the gland-cells had discharged their contents in the former and retained them in the latter, but if this were so there should be more evidence of the granules staining with haematoxylin than there is.

Dr. Baylis has very kindly examined the slides made of *L. ruber* described from Saldanha Bay in 1934. He writes : ' There are two series of transverse sections of *L. ruber*. In one of these (a single slide) the sections seem to have taken the haematoxylin fairly well ; in the other (several slides) there is hardly any haematoxylin, and therefore eosin predominates all over the sections. In the single slide the nuclei of the epithelial cells are quite well stained with haematoxylin. In both series, however, the epithelium contains masses of a secretion (mucus ?) which has taken up the eosin pretty heavily. These masses are seen not only in the epithelial layer itself (probably inside goblet-like cells) but also as blobs on its external surface. They thus give a considerable amount of eosin colour to the epithelium. It is interesting to find that in some sections of the same species from Millport made by the late Col. J. Stephenson, and apparently stained with some carmine stain, these same masses of secretion are very conspicuous '. On these characters I therefore feel justified in reinstating Stimpson's species *olivacea*.

LINEUS ORNATUS, sp. n. (SAN 4).

Four specimens of this worm, described as 'green, fairly common under stones' were preserved from Reef Bay, Port Elizabeth on July 5, 1936 (E.27).

In spirit the specimens are coiled, usually in a flat spiral at the tail with the lower surface inside. The bodies are not much flattened, the heads are rounded in outline from above and the succeeding part of the body is nearly round in section. Contraction wrinkles mark the surface of the body and longitudinal wrinkles occur at the anterior end behind the head. The colour is uniform black-grey, blue-grey, or green-grey. The cephalic slits are lined with white and a white band passes across the head from near their hinder ends. This band is not complete ventrally round the head (fig. 4, A). The lips are white and the mouth is pursed. It is rather more than 2 mm. long. No eyes are visible. The preserved specimens bear a striking resemblance to *L. corrugatus* M'Intosh, type iii, from the subantarctic regions (Wheeler, 1934).

The size, number of eyes, and sex of the specimens are given below :—

Length, cm.	Width, mm	Depth, mm.	Number of eyes.		Sex and maturity.
8·3	4·5	2·5	24	19	Female with ripe eggs.
4·8	4·5	2·5	15	16	Female, immature.
3·8	4·5	2·5	6	4	Not sexed, immature.
2·5	2·5	2·3	15	16	Male, immature.

The eyes are immediately visible in cedar oil (fig. 4, A) and are probably easily seen in the living animal. The presence of eyes distinguishes them completely from *L. corrugatus* (see note on p. 48).

There is a vertical cleft at the tip of the head in addition to the horizontal cephalic slits. No frontal organs are present. The cephalic slits are very deep and narrow (fig. 4, B). The head-glands are more massed together than is usual in the Lineidae : they stain palely with haematoxylin and contrast strongly with the deeply stained glands of the cutis. They persist at the slits until the latter disappear. The eyes are beneath the cutis-glands and close to the cephalic slits on their dorsal side. They contain brown pigment-granules and measure 0·05 mm. in greatest diameter.

In each angle formed by the cephalic slits and the epithelium small collections of unstained glands occur. They are similar to those described in *L. lacticapitatus*, though much less conspicuous.

The epithelium of the head is thin (0·05 mm.) and full of eosinophile glands. Anteriorly on the body it is slightly thicker (0·055 mm.) but similar in structure. The basement-membrane is 0·015 mm. thick and the cutis 0·05 mm. At the head the cutis contains mostly eosinophile glands, but behind the posterior end of the mouth the majority of the glands are deeply stained with haematoxylin and only few eosinophile ones occur (fig. 4, C).

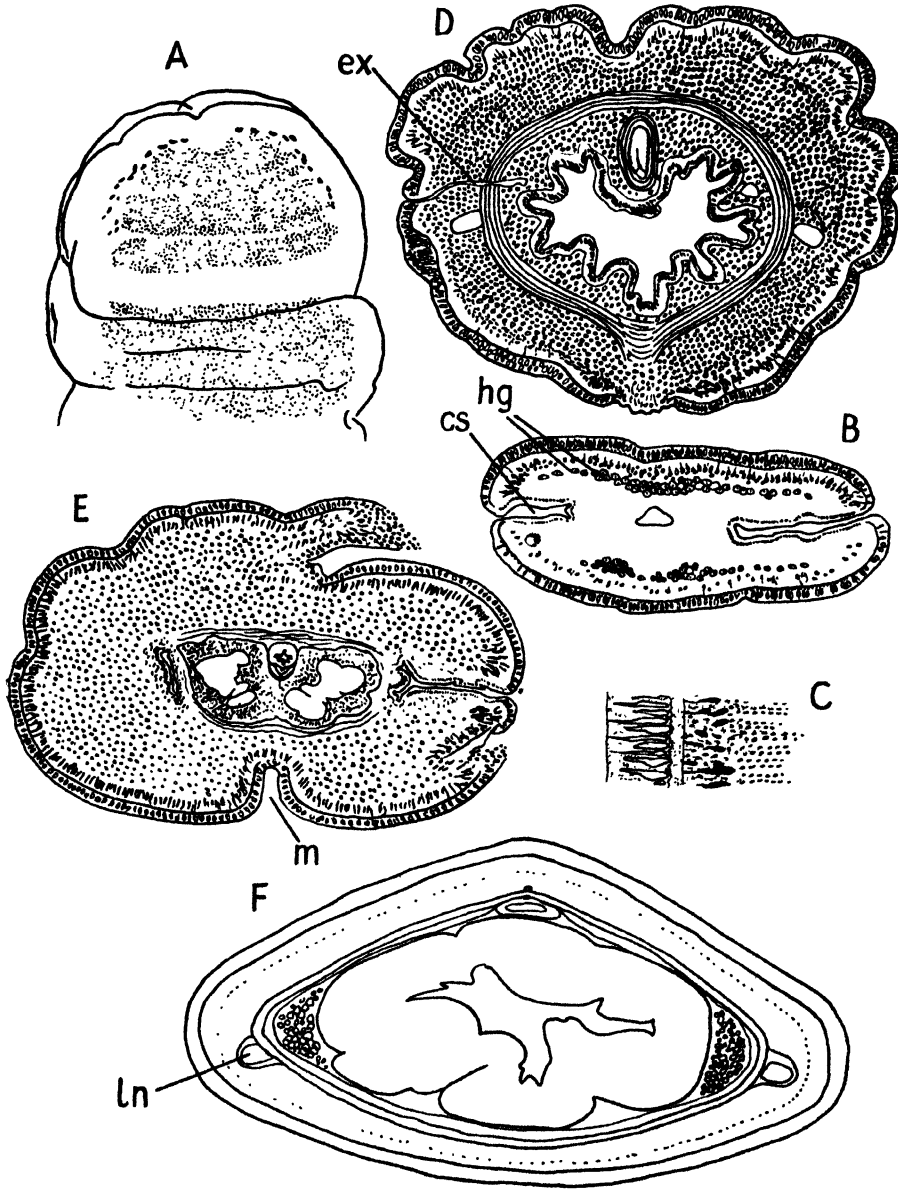

FIG. 4.—*Lineus ornatus*, sp. n.

A. Head of one of the specimens after clearing in cedar oil, dorsal view. B. Transverse section at the anterior end of the head, to show head-glands (*hg*) and cephalic slits (*cs*). C. Dorsal body-layers at the anterior end of the mouth. D. Transverse section of body at posterior end of mouth (*m*) showing one excretory duct (*ex*). E. Transverse section through brain. F. Hand-section through posterior third of body to show position of the lateral nerves (*ln*).

The excretory tubules occur close behind the cerebral organs, and a single duct on each side opens close behind the posterior end of the mouth laterally above the lateral nerves (fig. 4, D). The brain is small in relation to the size of the head, but is typically Lineid in structure (fig. 4, E). No neurochord cells are present. In the posterior part of the body the lateral nerves are almost in the horizontal plane of the body passing through the widest part (fig. 4, F).

This worm was the *Lineus corrugatus* previously identified (Stephenson, Stephenson and du Toit, 1937, p. 375). In view of the internal structure, especially the presence of eyes, this identification can be definitely cancelled. I can find no description of a worm comparable to this form. It approaches *Lineus indicus* Punnett & Cooper, (1909) but lacks the gelatinous layer beneath the cutis that is well marked in this species.

L. ornatus is characterised by its Lineid form, green colour in life, white margin to the cephalic slits, and white band across the top of the head, 4 to 24 dark eyes on each side at the edge of the pigment, deep narrow cephalic slits with glandular tissue on each side, and a small brain.

LINEUS RUBER (O. F. Muller) (SAN 3 & 9).

Two specimens were included in the collection : F.284 and F.283 (A), both from St. James, False Bay, on August 2, 1936. The note attached to the former was ' brick red, in sand under stone, rare ' and to the latter ' salmon pink, in sand under stone, rare '.

In spirit the length of SAN 3 is 12·5 cm. and the diameter 2·0 mm. ; SAN 9 is 6·8 cm. long and 1·0 mm. in diameter. The body is round in section, tapering towards the tail, which is pointed. The head is blunt. The colour is dark brown in places, with traces of violet, lighter brown underneath except at the head end. The tip of the snout is pale. The straight, well-marked cephalic slits are without a white lining. In SAN 9 most of the epithelium is missing, but patches of dark purple-brown colour remain at the tail. The mouth is a small sunken pit at the level of the hinder ends of the cephalic slits. No caudal appendage is present and no eyes are visible.

In cedar oil no eyes could be seen, but in SAN 3 a patch of reddish brown occurred at the junction of head and neck.

Frontal organs and eyes are present. The head-glands are diffuse and stain deeply with haematoxylin (fig. 5, A).

The epithelium is thin (0·045 mm.) and everywhere appears brilliantly stained with eosin. It is closely packed with flask-shaped gland-cells. There is a clear space about one and a half times the thickness of the epithelium between it and the cutis-layer, and this layer is about 0·1 mm. thick. In front of the brain the ventral glands are about equally eosinophile and stained with haematoxylin ; behind the brain the latter predominate (fig. 5, B, C).

The brain is large, and the cephalic slits are wide but not deep (fig. 5, D). The gonads (SAN 9 was a young female) extend at the sides of the gut and the

lateral nerves are just below the horizontal plane (fig. 5, E, F, G). An account of the anatomy has already been given (Wheeler, 1934), and in this paper the character of the epithelial glands has been emphasized to distinguish this species from the closely related *L. olivaceus*.

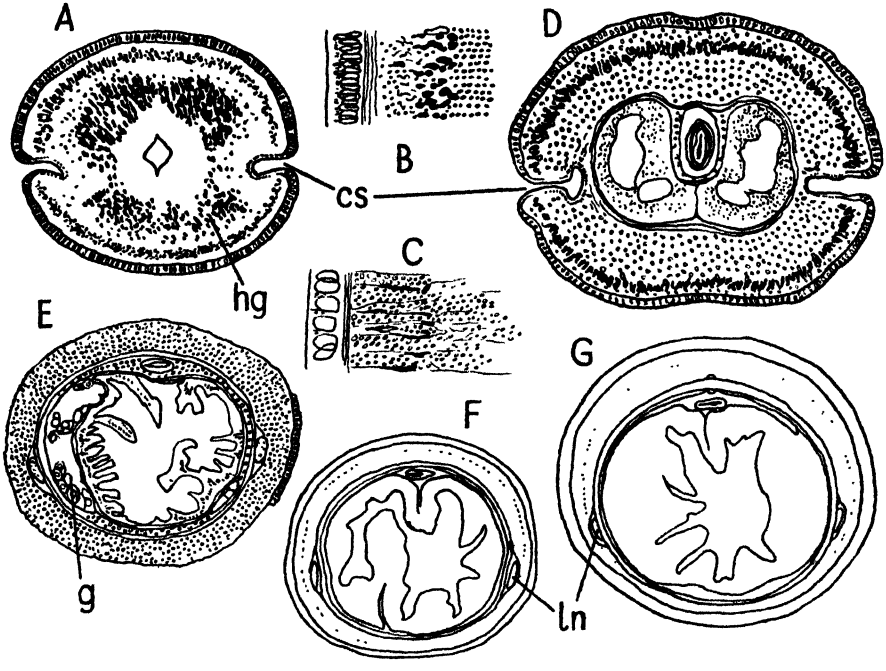

FIG. 5.—*Lineus ruber* (O. F. M.).

A. Transverse section through anterior end of head, to show head-glands (*hg*) and cephalic slits (*cs*). B, C. Dorsal body-layers, SAN 3 & 9, for comparison with fig. 3, E, F. D. Transverse section through brain. E. Transverse section (SAN 9) to show position of gonads (*g*). F, G. Hand-sections through posterior third of body, SAN 9, SAN 3, to show position of lateral nerves (*ln*).

Genus CEREBRATULUS Renier.

CEREBRATULUS FUSCUS M'Intosh (SAN 1, 7 *a* & *b*).

One specimen (F.216) from St. James, False Bay (April 11, 1933) was described as ' broad, pink, in pool, rare '. Two specimens from Oudekraal (June 28, 1934) were described as ' pinkish grey, under stone '.

In spirit all three specimens had partly autotomised, the first to the extent of a small part of the tail 4 mm. long ; both the others in two places, and in one of them the tail was missing altogether. In the first a caudal appendage was present ; in the other complete worm the end of the body was pointed and no appendage could be seen.

The colour is pinkish brown and uniform. The body is a flat oval in section, with strong lateral ridges in SAN 1 (an immature female), flattened dorsally and strongly convex ventrally in SAN 7 (a female with ripe eggs) (fig. 6, B, C). The size of SAN 1 was as follows :—Length 3·5 cm., breadth behind the head 4·0 mm., thickness behind the head 2·5 mm., broadest part of the body 5·5 mm.

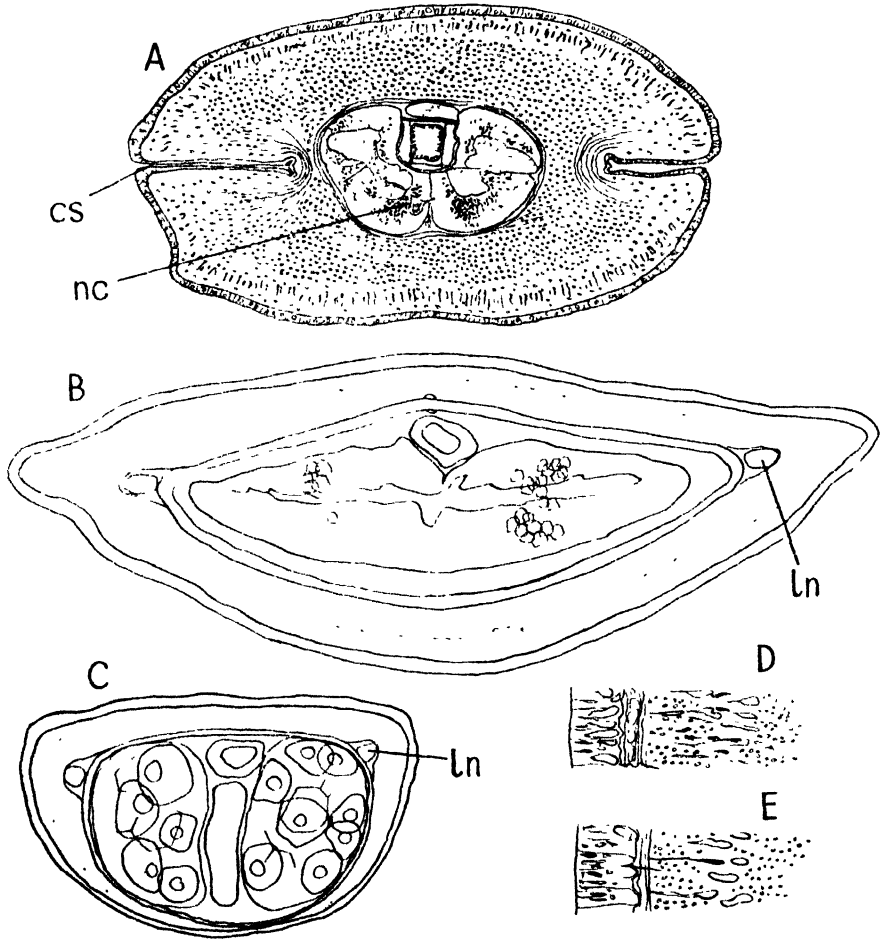

FIG. 6.—*Cerebratulus fuscus* M'Intosh.

A. Transverse section through brain region, to show cephalic slits (*cs*) and neurochord cell (*nc*). B, C. Hand-sections through posterior third of body of SAN 1 and SAN 7 to show position of lateral nerves (*ln*). D, E. Dorsal body-wall of SAN 1 & 7.

In this specimen the proboscis was extruded, 2·3 cm. long, 1 mm. in diameter, and pale pink in colour. The other specimens were approximately 2·5 cm. long and 2·0 and 1·8 mm. broad.

The head is somewhat triangular in outline from above, very acutely pointed from the side. Narrow cephalic slits are visible, succeeded on the body by a distinct lateral longitudinal ridge. The body is transversely wrinkled, with longitudinal wrinkles visible behind the head. No eyes can be seen, nor do any become apparent on clearing in cedar oil. The mouth is small. Hand sections show that the rhynchocoel extends well into the posterior third of the body.

Frontal organs are present. Eyes are present in the form of deeply-placed brown cup-shaped structures. Head-glands are sparse, stain palely with haematoxylin and nearly reach the brain. The cephalic slits are deep.

A description of *C. fuscus* from Saldanha Bay has already been given (Wheeler, 1934), and to this description these worms conform, with the additional fact that a pair of neurochord cells is present (fig. 6, A). The cells have been found in both series of sections, and in the more favourable it is evident that each cell is bipolar, one branch passing into the ventral fibres of its own side, one passing across to the other. The co-ordination of the muscles necessary for the action of swimming inevitably suggests itself in connection with the presence of neurochord cells in *Cerebratulus* as opposed to their absence in the creeping Lineids.

The outline sections through the posterior third of the body (fig. 6, B & C) show that the convexity of the ventral side causes the lateral nerves to appear above the median horizontal plane. Actually the nerves are at the broadest part of the body and at the true lateral margins.

Order HOPLONEMERTEA Hubrecht.

Suborder MONOSTYLIFERA Brinkmann.

Genus EMPLECTONEMA Stimpson.

EMPLECTONEMA OPHIOCEPHALUM (Schmarda) (SAN 13).

One specimen of a very long white worm, found under a stone in a pool at Oudekraal on July 28, 1934, has been identified with a species described from Saldanha Bay, which was shown to be the form discovered by Schmarda under stones and in sand at Table Bay and named by him *Ommatoplea ophiocephala*.

In spirit the specimen is 22·0 cm. long, 2 mm. wide, and 1 mm. thick. It is whitish grey in colour and marked by chalky-white dots indicating the presence of gonads throughout the body from 12 mm. behind the head to 5 mm. from the tip of the tail. The head end is thick and blunt, the tail bulbous and bluntly pointed. A few circular wrinkles occur behind the head, and a mid-dorsal depression passes down the body. No grooves are apparent on the head, and no eyes are visible even on clearing in clove oil. The tightly apposed right and left brain-lobes and the short proboscis, with the base of the main stylet (0·06 mm.), can be seen.

Many eyes are immediately visible in sections (fig. 7, A). The head-glands disappear at the junction of the oesophagus and rhynchodaeum. The connective tissue of the body stains with haematoxylin, as noted previously.

The basement-membrane is thick and stains with haematoxylin. The epithelium is also thick, but in this specimen is practically entirely missing except for a few patches at the tail. The eggs are large and each contains one pair (fig. 7, B). The form of the brain, the small size of the cerebral organs and their disappearance before the brain, and the staining of the connective tissue leave no doubt as to the identity of this specimen.

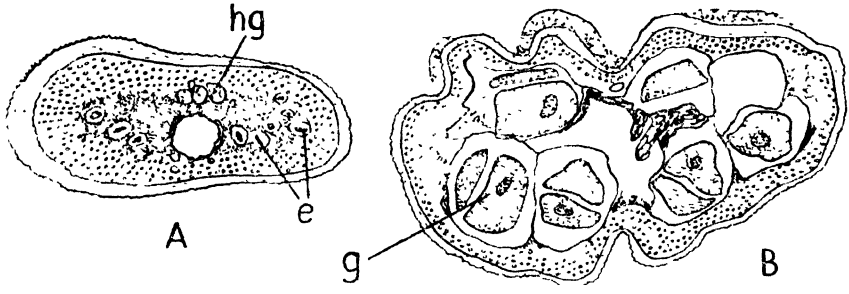

FIG. 7 *Amplectonema ophiocephalum* (Schmarda).
A. Section through anterior end of head, to show eyes (*e*) and head-glands (*hg*).
B. Section of body near tail, showing the paired ova (*g*).

Genus ZYGONEMERTES Montgomery.

ZYGONEMERTES CAPENSIS Wheeler (SAN 14, 17).

Two specimens occur in the collection: one 'white in colour, living among the "roots" of the holdfast of a plant of the sea bamboo, *Ecklonia buccinalis*, in a very deep pool' at Oudekraal (A 174 *a*), taken on March 17, 1934; the other (SAN 17) 'pink in colour, two found under stones in channel in the middle part of the shore' at Shelly Beach, East London, on July 25, 1937 (L 414).

Both preserved specimens are slender, without markings. The former is white, the latter pale buff-grey. The body tapers in each, the lengths being 3·0 cm. and 3·6 cm., the width (a little less than the thickness) being about 1 mm. The head is little flattened, round in outline from above and bears a distinct chevron groove at the back with the apex pointing down the body (fig. 8, A). There is a second ring-groove some distance further back in both. No eyes or slits can be distinguished, but eyes appear in cedar oil in the three groups, the outer anterior group opening forward, the inner back, and the posterior laterally as previously described. In both the characteristic hooks are present in the epithelial cells (fig. 8, B).

The anatomy follows the previous description, with the exception that in SAN 17 the proboscidial nerves number 14–15, whereas in the type they were thirteen. In SAN 14 the proboscis is missing. Further, the single excretory

duct on each side, which lies close behind the brain, opens to the exterior directly downwards under the lateral nerve instead of laterally from above it. In the section drawn (fig. 8, C) the head was cut obliquely, so that the dorsal commissure is shown in addition to the dorsal ganglia, while the ventral ganglia have already become the lateral nerves. This accounts for the position of the excretory ducts very far forwards in the brain-region. I do not know whether the difference in the course of the excretory ducts is of significance. It is possible that had the thick proboscis been retained the gut would have been pressed downwards and the ducts would then appear lateral, or that, as in *Amphiporus africanus*, there are more ducts than one and they do not pass to the exterior in the same direction. SAN 14 is a ripe male with testes as shown in the original description (Wheeler, 1934, p. 342, fig. 15, B). SAN 17

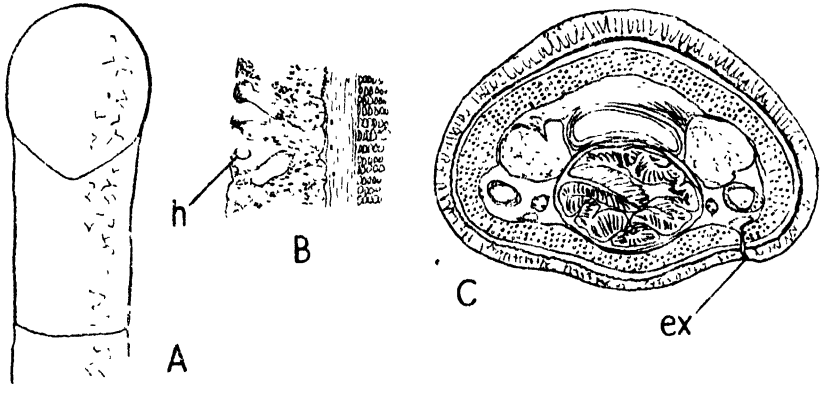

FIG. 8.—*Zygonemertes capensis* Wheeler.

A. Head of SAN 14. B. Body-wall in region of anterior caecum, showing one of the characteristic hooks (*h*). C. Transverse section of body in the region of the excretory duct (*ex*).

is a ripe female with very large eggs. In this specimen the armature was seen. The main stylet is 0·06 mm., the base 0·14 mm., brownish in colour and square at the end. Two accessory reservoirs could be discerned, but no stylets. The rhynchocoel extends the whole length of the body. This fact, with the hooks in the epithelium and the position of the groups of eyes, justifies the inclusion of this specimen under *Zygonemertes*.

Genus AMPHIPORUS Ehrenberg.

AMPHIPORUS AFRICANUS, sp. n. (SAN 11, 18).

Two specimens of this species were collected, SAN 11 'a small white worm, living between the roots of the alga *Hypnea specifica*, low down on the shore' at Shelly Beach, East London, on July 7, 1937 (L 108); and SAN 18 'a small

pink worm, under stone in channel on the upper part of the shore ' at the same place on July 20, 1937 (L 343).

In spirit the first specimen is of a very pale pinkish-mauve colour, the body twisted and mottled and dotted with white gonads. It is approximately 1·8 cm long, 1·8 mm. wide at the head, and 1·5 mm. thick. Circular wrinkles occur at the head (fig. 9, A) and there is a pore at the extreme tip. The second specimen is shorter, 7·0 mm long, 1·5 mm. broad, and 1·0 mm. thick. The head

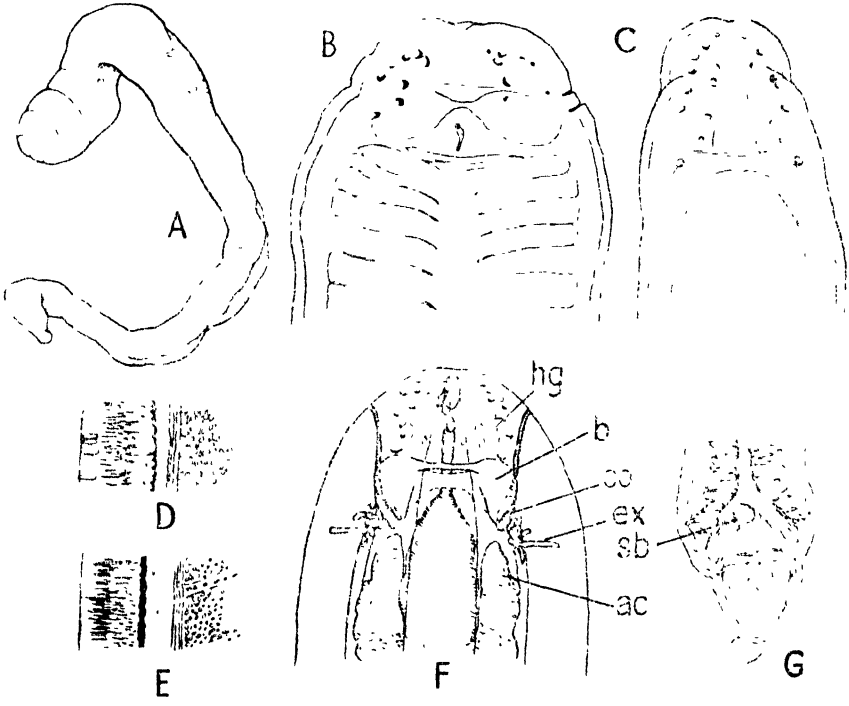

FIG. 9. *Amphiporus africanus*, sp. n.

A. Sketch of preserved specimen, SAN 11. B. Head of SAN 18, cleared in cedar oil. C. Head of the *Amphiporus* from Saldanha Bay, sketch made in 1933. D, E Body-wall in region of anterior caecum. F. Graphical reconstruction of the head from sections of SAN 11 and 18, showing head-glands (*hg*), brain (*b*), cerebral organs (*co*), anterior caecum (*ac*), and excretory duct (*ex*). G. Longitudinal section of part of the proboscis, to show the base (*sb*) of the main stylet.

is round and there is a very well-marked circular fissure round the body behind it with slight transverse wrinkling. The body tapers and the tail ends abruptly. Neither mouth nor eyes can be seen. In cedar oil no eyes can be distinguished in SAN 11, but in SAN 18 there are eight pale brown cup-shaped eyes on each side in two irregular lines near the margin of the head. The branches of the gut are simple and the brain is large (fig. 9, B).

In SAN 11 thirteen eyes altogether were counted in the serial sections. The rhynchocoel extends to the end of the body. The proboscis, which had been retained, has eleven nerve-strands, a short round red base to the main stylet (fig. 9, G), and two accessory reservoirs. None of the stylets had been preserved. The epithelium in the region of the anterior caecum stains lightly with haematoxylin. It is 0·055 mm. thick and lies over a deeply-stained layer, apparently distinct from the thick basement-membrane, which appears homogeneous and stains lightly with eosin. Beneath this are the two muscle-layers of the body. The circular layer is 0·01 mm. thick. There is no diagonal layer.

The head-glands are diffuse, do not stain, open to the rhynchodaeum close to its external opening and disappear just before the brain (fig. 9, F). The narrow oesophagus opens into the rhynchodaeum close to the external opening of the latter. Directly behind the brain it widens into a capacious mid-gut. An anterior caecum is present, and two branches reach forward to the posterior end of the brain.

The excretory system is directly behind the brain, and the ducts to the exterior occur here also (fig. 9, F). In SAN 11 there are two ducts above the lateral nerves passing outwards and slightly upwards, and two below, passing downwards on the left side ; on the right there is a single duct above the nerves. In SAN 18 one duct passed out laterally and one ventrally on the left, on the right a single duct passed out laterally just ventral to the plane of the middle of the body. The cerebral canals open laterally just in front of the brain. They pass in and back along the sides of the brain between the dorsal and ventral ganglia until the latter become the lateral nerves. They then expand into the cerebral organs and continue past the ends of the dorsal ganglia (fig. 9, F). The lateral nerves in both specimens make an abrupt turn outwards at the brain, and an equally abrupt turn to pass down the body.

Both specimens were females, SAN 11 having larger oocytes than SAN 18. In both the cytoplasm of the smaller oocytes is stained with haematoxylin, that of the larger with eosin. All contain a deeply stained (purple) nucleolus in each nucleus, which appears enormous in the smallest oocytes and is actually smaller in the larger ones. Several oocytes occur together in each sac, and the latter occur regularly between the branches of the gut.

The only *Amphiporus* taken at Saldanha Bay was identified with *A. pulcher* Johnston. This possessed eleven nerves in the proboscis. It differed from those here described only in the position of the two branches of the anterior caecum, which in the previous specimen did not approach the brain, and in the course of the excretory ducts, which passed back and opened laterally some distance behind the brain. These differences are explained by the different states of contraction of the body. In the Saldanha Bay specimen ' the ventral ganglia, becoming the lateral nerves, shift gradually outwards ', while in the present specimens there is a double twist. This is shown in two sketches of the heads of animals, one from Saldanha Bay (fig. 9, C) and one from the present material

(fig. 9, B, SAN 18). In the latter contraction has brought the anterior caecum close to the brain, and doubtless the excretory ducts as well.

There are differences between these animals and *Amphiporus pulcher* in the number of nerves in the proboscis and the branching of the gut. Bürger (1904) gives ten nerves in *A. pulcher* and states that the pockets of the gut are branched (1895, p. 567). The occurrence of eleven nerves in the proboscis and the simple gut-branches justify the new species *Amphiporus africanus*, in which is included the form previously described from Saldanha Bay as *A. pulcher*.

Genus Prostoma A. Dugès

Prostoma dutoiti, sp. n (SAN 16).

One specimen was taken at Bats Cave Rocks, East London, on July 17, 1937 (L.512), with the note 'only one found living in a little hole in the soft limestone of which the littoral rocks are composed'.

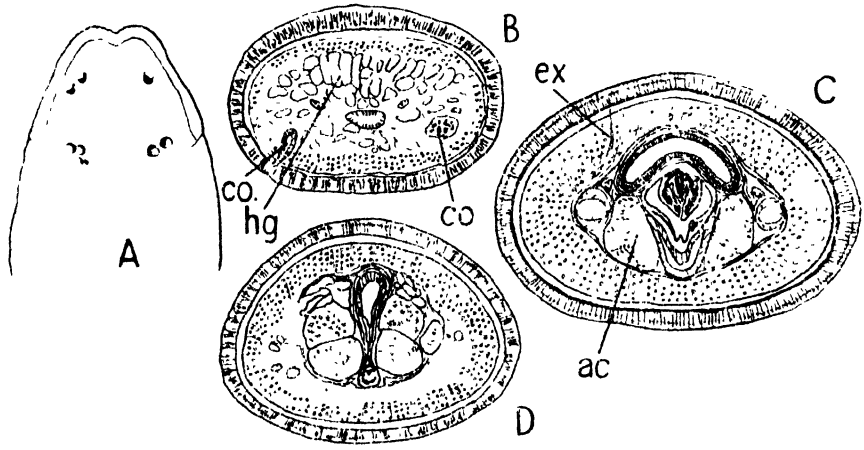

Fig. 10 - *Prostoma dutoiti*, sp. n

A. Head cleared in cedar oil. B. Transverse section through anterior end of head, to show head-glands (*hg*) and cerebral organs (*co*). C. Transverse section of body, showing branches of the anterior caecum (*ac*) and excretory duct (*ex*). D. Transverse section through brain, to show extent of head-glands.

The preserved specimen is a thin brown worm with a thread-like proboscis nearly as long as the body. The tip of the head appears white, and a small elevation just beneath the tip marks the opening of the rhynchodaeum. The length is 1·7 cm., breadth 1 mm., and thickness 0·5 mm. The proboscis is about 0·03 mm. in diameter. The head is pointed and somewhat flattened, the tail acutely pointed. On clearing in cedar oil the eyes are visible as large brown cup-shaped bodies, in groups of two and four on the left and one and two on the right, at the angles of a rectangle (fig. 10, A). The stylets had been

dissolved, but the base of the main stylet is small (0·05 mm.) and pear-shaped.

The head-glands open at the tip of the head near the rhynchodaeum. They are large and continue back to the brain. There is a mass over the dorsal ganglia which almost disappears with the ganglia; but isolated strands continue behind the brain (fig. 10, B. D).

The epithelium is thick (0·05 mm.) and is packed with haematoxylin-stained nuclei at the bases of the cells and elongated bodies further out. The basement-membrane stains deeply and is thinner than the circular muscles (0·01 mm.). The oesophagus is very narrow in the brain region. It opens out afterwards to a simple tube with deeply-staining cells in the walls. Two symmetrical branches of the anterior cæcum pass forwards, at first closely pressed beneath the gut, further forwards separated by it (fig. 10, C) and ending some distance behind the brain. The rhynchocoel extends to the posterior third of the body at least, and the proboscis possesses thirteen nerve-strands. The cerebral canals open at the tip of the head near the proboscis pore (fig. 10, B), and the organs disappear before the brain. Two ducts on one side passing directly upwards, one behind the other, some distance behind the brain, constitute all that is seen of the openings of the excretory system (fig. 10, C). The brain is large. No neurochord cells are present, and the dorsal ganglia are not continued in the lateral nerves as in *Oerstedia maculata*, described from Saldanha Bay.

Duplication or multiplication of the eyes is not uncommon in this genus. Bürger (1895) has described *P. cruciatum* from Naples with four double eyes; Coe (1905) described *P. aberrans* from Alaska in which the eyes were 'three to five isolated pigment masses of variable size', and I have described *P. osbenseni* from South Georgia and *Oerstedia maculata* from South Africa with a larger number than the usual four of the genus. The increase in the number of eyes appears to be often accompanied by an increase in the number of nerves in the proboscis. Coe remarks on the twelve nerves in *P. aberrans*.

P. dutoiti can be separated from *O. maculata* by the possession of thirteen nerves in the proboscis instead of ten, the branched anterior caecum, and the greater extent of the head-glands. I have named the species in honour of Dr. C. A. du Toit, associated with Professor Stephenson in the ecological survey.

Suborder POLYSTILIFERA Brinkmann.

Genus PARADREPANOPHORUS Wijnhoff.

PARADREPANOPHORUS STEPHENSONI, sp. n. (SAN 2, 12).

Two specimens were collected at Oudekraal, A.395 (SAN 2) on October 7, 1934, and A.101 (SAN 12) on January 18, 1934. In life the former was noted as 'stout, pinkish, from North Rocks, Oudekraal, under stone in pool', the latter as 'pinkish in colour, under stone in fairly deep pool'.

SAN 2. Length 5·2 cm.; broadest part of body 3·8 mm.; thickest part of body 2·0 mm.

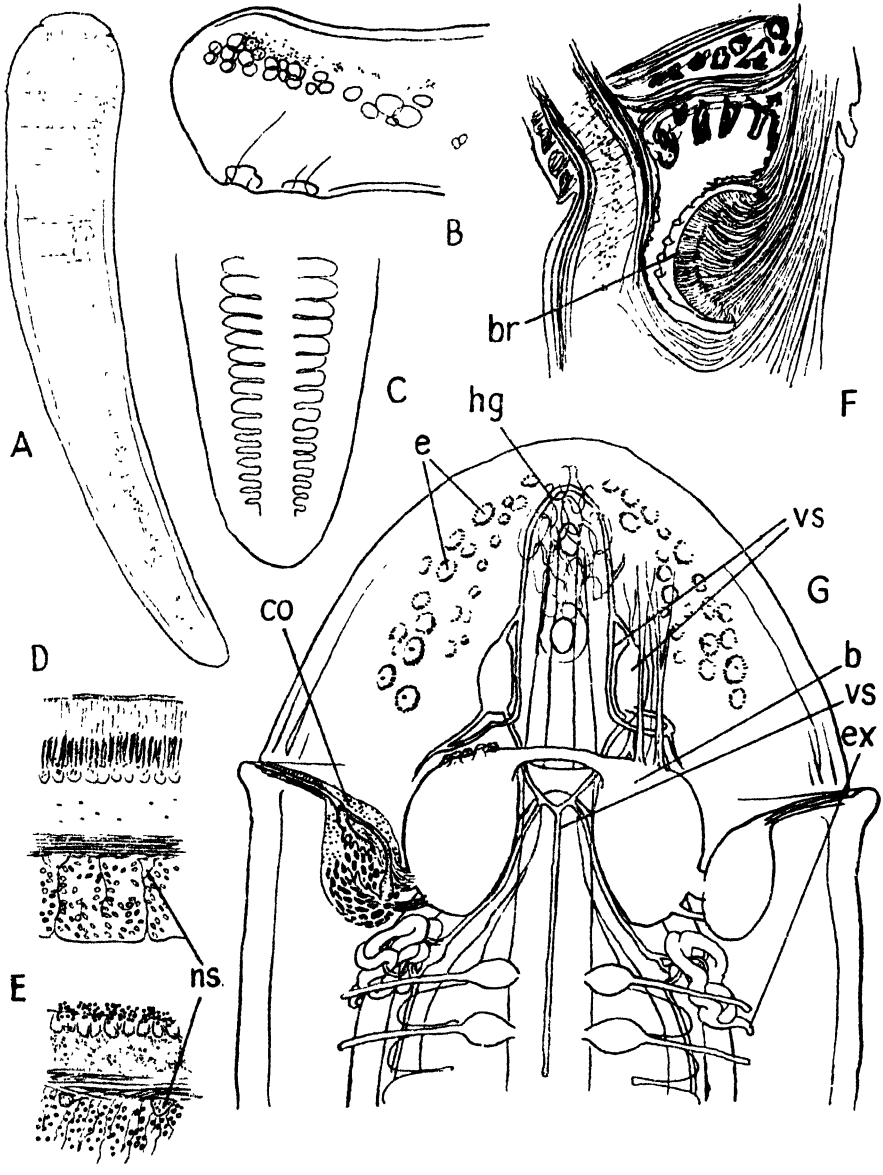

FIG. 11.—*Paradrepanophorus stephensoni*, sp. n.

A. Sketch of preserved specimen, SAN 12. B. Head of SAN 2, side view, after clearing in cedar oil. C. Tail of SAN 12, after clearing in cedar oil. D, E. Body-wall of SAN 12 (brain region) and SAN 2, showing the nerve-strands (*ns*) beneath the basement-membrane. F. Longitudinal section of the stylet region of the proboscis reconstructed from two sections, to show the basal rod (*br*). G. Graphical reconstruction from both series of sections, showing head-glands (*hg*), eyes (*e*), vascular system (*vs*), brain (*b*) and cerebral organs (*co*), alimentary and excretory systems (*ex*).

SAN 12. Length 1·7 cm.; broadest part of body 3·0 mm.; thickest part of body 1·0 mm.

Both the preserved specimens are uniform light brown in colour. The head is bluntly rounded in outline from above, and the succeeding part of the body is nearly round in section. A short distance behind the head the body becomes progressively more and more flattened, and distinctly sharp edges appear. The tail is so thin that it is translucent (figs. 11, A, C). In SAN 2 faint blackish areas on the dorsal side of the head indicate the eye-spots. In cedar oil eighteen large pale brown cup-shaped eyes were counted on the right side, with a smaller group nearer the middle line (fig. 11, B). In SAN 12 no eyes could be seen, probably because this worm had retained the thick epithelium. Branches of the gut, as short lateral pockets, can be seen reaching about halfway from the middle line to the edge of the body (fig. 11, C).

SAN 2 had contracted little; SAN 12, on the other hand, had retracted the head very considerably, making the tracing of the alimentary and vascular systems difficult. SAN 2 had lost the epithelium over the anterior part of the body and head, and the proboscis was missing, but both epithelium and proboscis were present in SAN 12, the proboscis having been detached but retained with the body. In certain particulars there are differences between these specimens. The basement-membrane appears to be thicker in SAN 12, and the anterior caecum and excretory ducts are closer to the brain, but I am satisfied that such differences are due to the different states of the animals on preservation.

The epithelium is thick (0·08 mm.) and contains elongated bodies staining deeply with haematoxylin towards the basal part of the layer. The basement-membrane (0·065 mm.) stains palely and overlies the circular muscles (0·035 mm.) and a layer of crossed diagonal fibres (fig. 11, D, E). The longitudinal muscles are separated, though not conspicuously, into bundles, and between these, close under the diagonal muscle-layer lie longitudinal nerve-strands. These are very striking in SAN 2 (fig. 12, A, B, D, H) and present, though not so evident, in SAN 12. Just before the opening of the cerebral canal there are five longitudinal furrows in the epithelium, lined with modified cells. These abut on a transverse fold (fig. 12, F). In SAN 2, owing to the absence of the epithelium, the furrows are not evident. The head-glands (fig. 12, A, C) are compact, do not stain, are placed mid-dorsally over the rhynchodaeum and disappear over the opening of the oesophagus. The aperture is terminal. The eyes are large. In the sections I counted 24 on one side, 29 on the other in SAN 2; 19 on one side, 16 on the other in SAN 12. The larger ones lie nearer the margins of the head, suggesting that in the living animal there are four rows of eyes diverging from the tip of the head.

The mouth and proboscis-pore are separate (fig. 11, B, SAN 2). There is a unique but very definite connection between the opening of the rhynchocoel and the oesophagus in the form of a flattened tube, as shown in the three sections drawn (fig. 12, A, B, D). In SAN 2 both openings are very distinct, as can

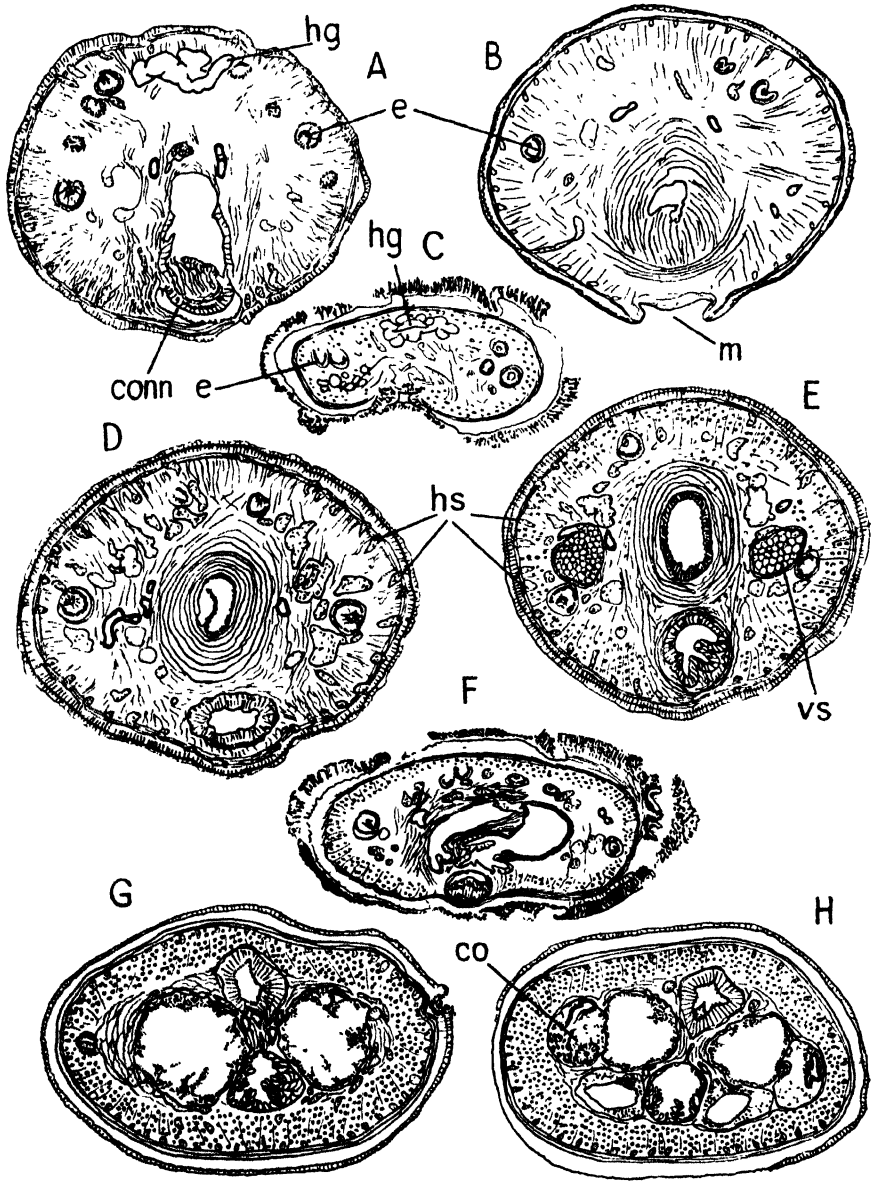

FIG. 12.—*Paradrepanophorus stephensoni*, sp. n.

A, B, D, E, G, H. Sections of the series SAN 2, showing the head-glands (*hg*), eyes (*e*), connection (*conn*) between the proboscis-pore and mouth (*m*), peripheral nerve-strands (*ns*), vascular sacs (*vs*), brain and cerebral canals (*cc*) and organs (*co*). For comparison the sections C and F of the series SAN 12 are given.

be seen from the side view of the head cleared in cedar oil (fig. 11, B). In SAN 12 there is more of an atrium, due partly, though not entirely, to the presence of the epithelium. Notwithstanding the distortion due to contraction in this specimen, the connecting-tube can be traced. It is as though the lips of a narrow elongated atrium joining the proboscis-pore and mouth had coalesced.

The oesophagus continues back to the brain as a simple tube. Directly behind the brain it expands and its walls become folded (fig. 12, H ; fig. 13, E). A capacious simple anterior caecum stretches forwards 0·5 mm., giving off on each side simple pocket-like diverticula in continuation with the intestinal series (fig. 13, A, B, F).

The vascular system is composed of well-marked vessels. There is a loop vessel in the head which passes back on each side of the rhynchocoel. In front of the brain these vessels divide, the outer branches enlarging and forming conspicuous ovoid sacs in both series of sections. The sacs are filled with nucleated bodies (figs. 11, G ; fig. 12, E). Each sac has a fine muscular investment and each opens posteriorly into two vessels, both passing back. One of these rejoins the other branch of the head loop, and traces of it are soon lost outside the brain ; the other passes in and enters the nerve-ring. Here it joins the vessel from the other side of the body and gives off the dorsal vessel, which almost immediately passes upwards through the rhynchocoel wall, and the lateral vessels, which pass down the body on each side in association with the lateral nerves (fig. 11, G). At the region of the excretory tubules the lateral vessels become convoluted, and enlarged sacs are again to be seen in close proximity to the tubules. The dorsal vessel remains within the rhynchocoel until the second pair of sacs are given off from the anterior caecum, when it descends through the wall and runs dorsal to the gut. Neither commissural vessels, passing between the intestinal diverticula to the median dorsal vessel, nor vessels passing round the end of the diverticula, as described by Punnett (1901) in *Drepanophorus roseus*, can be seen. In *D. roseus*, however, the vascular system is described as being exceedingly conspicuous by reason of the large oval corpuscles contained in it. The ovoid sacs described above contain nucleated cells packed together so that the walls of the cells appear angular. They correspond with the blood-corpuscles figured by Bürger (1895, pl. vii, fig. 10) from *Drepanophorus crassus*, and are found only in the sacs—the vessels through the body are empty.

The excretory tubules form a convoluted mass directly behind the brain and cerebral organs. A single duct on each side, which passes over and outside the lateral nerve, opens on the ventral surface immediately below the nerve (fig. 11, G).

The proboscis is thick and white. It is 1·2 mm. in diameter and 5 mm. long (SAN 12). After clearing, the curved basal rod is visible, with eight angle-cups for the bases of the stylets (fig. 11, F). The proboscis has 22 nerve-strands. The rhynchocoel at first is without a muscular envelope. A

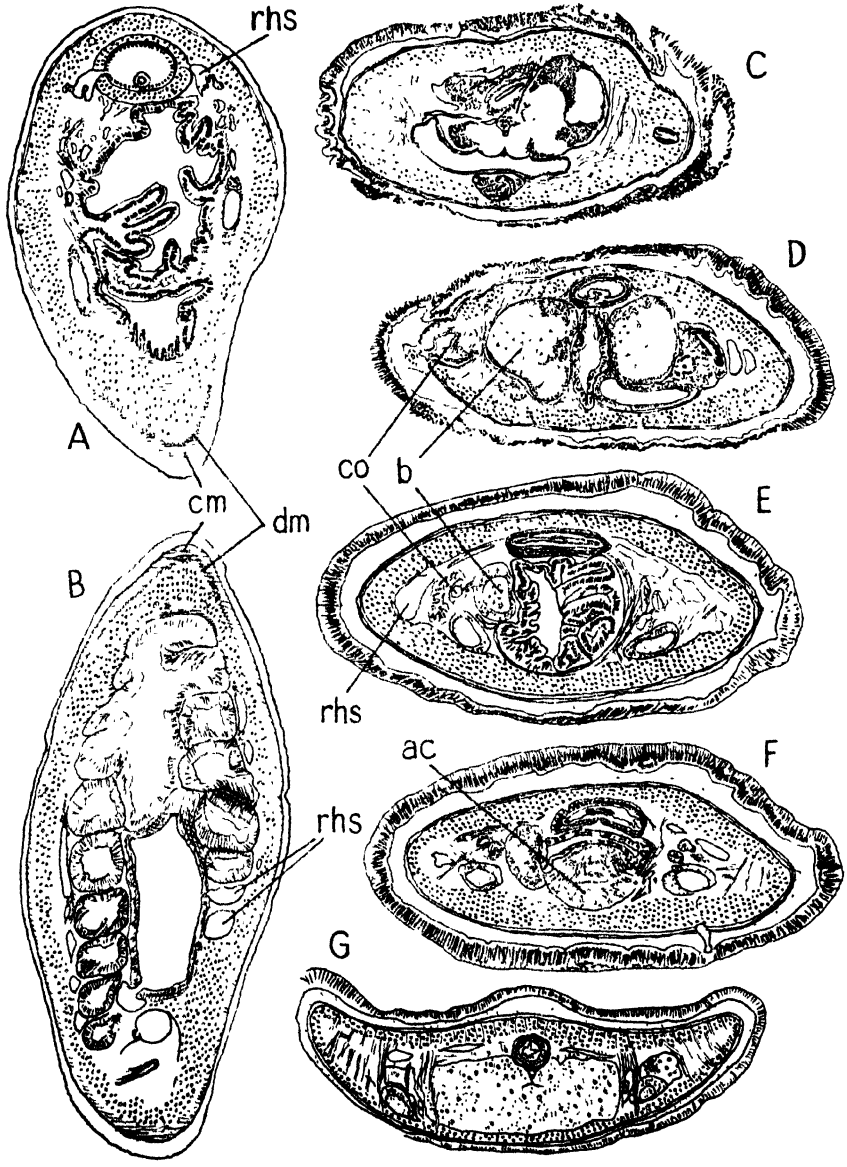

FIG. 13.—*Paradrepanophorus stephensoni*, sp. n.

A, B. Oblique section across a bend in the preserved specimen showing the diagonal muscle-layer (*dm*) beneath the circular muscles (*cm*), rhynchocoel sacs (*rhs*), and branches of the gut. C, D, E, F, G. Sections of the series SAN 12, showing the brain (*b*) and cerebral organs (*co*), anterior caecum (*ac*), excretory duct (*ex*), and shape of the posterior end of the body in transverse section.

sphincter surrounds it in front of the brain, and here the nerves enter the musculature. Further back the wall is formed of interlacing circular and longitudinal fibres. The paired diverticula are given off at each side, beginning behind the brain (fig. 13, A, E, F, G). In SAN 2 they appear to be short round sacs, but examination of oblique sections (fig. 13, B) shows that there is a proximal inflated part and a much longer distal narrow tubular part passing above the gut-branches and over the lateral nerves. In SAN 12 the proximal inflation is absent. Presumably the diverticula are extensible when the proboscis is withdrawn in life, and collapse when it is extruded. The diverticula alternate with the gut-branches.

The brain is very large. Dorsal and ventral ganglia are hardly distinguishable from one another, but the former are far larger than the latter. The fibrous part of the brain is much greater than the cellular part. I have distinguished a pair of neurochord cells in one worm (SAN 2) and one neurochord cell in the other. They occur on the mesial face of the dorsal ganglion, high up near the rhynchocoel wall, just before the ventral part of the fibrous tissue of the brain becomes independent and can be called the ventral ganglion. The dorsal ganglia are bi-cornuate posteriorly. The dorsal commissure is longer and thinner than the ventral, though I believe that fixed material does not give an adequate picture of the living tissue, owing to stretching by the passage of the proboscis and convulsive movements at the time of fixing. In SAN 12 the ventral ganglia take a sharp turn outwards to become the lateral nerves, and again turn sharply to pass down the body (fig. 13, D). In SAN 2 the lateral nerves shift outwards gradually, indicating that one worm was fixed in comparative relaxation, while the other contracted violently, and in doing so brought the mouth and proboscis pore close together, twisted the lateral nerves, reduced the distance of the excretory ducts and anterior caecum from the brain, and thickened the basement-membrane.

The cerebral canals open laterally in the brain region. After passing through the longitudinal muscles the canal forks. Ciliated cells occur in both branches, one of which passes dorsally. This branch ends in four or five short finger-like blind pits, which overlie the gland-cells that are associated with the other branch. At the fork of the canal and for a short distance beyond it the two branches are surrounded with nerve-cells and fibres. The latter can be traced into the dorsal ganglion. The ventral branch turns to pass parallel to the side of the dorsal ganglion. It becomes surrounded with eosinophile cells which appear to secrete into a main duct passing inwards to the end of this branch. The branch opens out and is invested in the fibres of a large nerve from the posterior end of the dorsal ganglion. The cerebral organs are rounded off by gland-cells (fig. 11, G). The lateral nerves pass down the body close to the ventral longitudinal muscles and about halfway between the middle line and the margin of the body on each side.

Both specimens were immature females. Few very small oocytes occur

in the simple gonadial sacs between the branches of the gut. In each oocyte a large dark globular nucleolus can be seen (fig. 13, G). The sacs are placed close to the lateral nerves on the mesial side. Dorso-ventral muscle-strands occur here between the gut-branches.

The Polystilifera have recently been the subject of an exhaustive treatise by Wijnhoff (1936), who divides the littoral creeping and swimming forms into two divisions depending on the structure of the cerebral organs. In a previous paper by Wijnhoff (1926) the distinction was summed up as follows :—' The presence of a cerebral sac is almost restricted to the Polystilifera Reptantia and involves the bifurcation of the cerebral canal. . . . In *Drepanophorus*, s.str., *Brinkmannia* and *Punnettia* the branch which opens into the sac has a sensory epithelium and communicates with the sac by a slit-like mouth along its whole length as described by Bürger. The same kind of sensory epithelium is found in the other canal which ends as a glandular tube. As a rule the dorsal canal is in connection with the glandular masses, the ventral one with the sac. In all other genera . . . the branches of the cerebral canal are unequal. The branch leading to the sac has no slit-like mouth nor sensory epithelium . . . whereas the glandular branch has a sensory epithelium. Moreover, the ventro-median one always goes to the glandular mass and the dorso-lateral one to the sac. . . .'

A comparison with some sections of *Punnettia hubrechti* Wijnhoff, made in Plymouth in 1921, with a colour-sketch that enabled identification to be made from Wijnhoff's table (1926) of the Mediterranean species shows clearly the difference in the types of cerebral organs. *Punnettia* belongs to the Equifurcata ; the animals described here to the Inequifurcata of Wijnhoff, which are thus diagnosed (1936)—' Mund und Rüsselöffnung liegen fast immer gemeinsam in einem Atrium. Der Cerebralkanal spaltet sich in einen Sinneskanal und einen Sack. Rhynchocolomdivertikel oft verzweigt. Gonaden oft mehrreihig. Gehirn mit Neurochordzellen '.

The assemblage of characters that distinguish the Paradrepanophoridae are—' Grosses Gehirn mit kurzer ventraler Kommissur und gut entwickelten ventral gelegenen aber kaum abgetrennten ventralen Ganglia. Dorsale Ganglia sehr gross. Einfache circuläre Kopffurchen. Cerebralorgane dem Gehirn angelagert, mit Neurilemma, ohne Anhänge. Keine Drüsen an der Gabelstelle. Unverzweigte Rhynchocölomdivertikel hinter dem Gehirn. Magen mit Blindsäcken. Darmtaschen unverzweigt. Gonaden mit ventralen Pori, oft mehrreihig '.

The new species, named in honour of Professor Stephenson, is characterised by the connecting-tube between the proboscis-pore and the mouth, by the dilated ovoid vessels in the head, and by the peripheral longitudinal nerves. In life it is a small form, uniformly pink in colour, with a broad body and with sixteen to twenty-nine eye-spots in the head.

Note on Lineus corrugatus M'Intosh.

The erroneous identification with *Lineus corrugatus* of the worms to which I have given the name *L. ornatus*, sp. n., in this paper has drawn my attention again to the confusion that exists regarding the presence of eye-spots in this species. Thus, Punnett and Cooper (1908) reported *L. corrugatus* from Cargados Carajos, near Mauritius in the Indian Ocean, remarking that the specimen 'agrees with the type in the presence of eyes . . .', yet in the table appended to their report classifying certain anatomical features of the Lineidæ eyes are denoted as absent in *L. corrugatus*.

L. corrugatus was originally described from the 'Challenger' collections at Kerguelen by M'Intosh (1879) and Hubrecht (1887). Neither found eyes. I have recently examined many specimens from the type-locality collected by the British, Australian, and New Zealand Antarctic Research Expedition, and I can find no trace of eyes on clearing in cedar oil or anilin oil or in sections.

In 1896 Bürger described *Cerebratulus magalhaensicus* from southern South America and the Falkland Islands. This species was said to possess a few small eyes near the cephalic slits. Several further records of the species occur in the literature (Bürger, 1896*b*, 1899, 1904*b*), but in 1907 Bürger himself synonymised his *C. magalhaensicus* with M'Intosh's *Lineus corrugatus* and bestowed upon it 'eine geringe Anzahl kleiner Augen, welche dicht vor den Kopfspalten liegen'.

On my way to South Georgia in 1924 as a member of the 'Discovery' Investigations staff I collected some worms in Port Stanley Harbour in the Falklands. They corresponded with the description of *C. magalhaensicus*, but were without eyes. Later, in South Georgia between 1925 and 1927 and again in 1931 I made many observations of living Nemerteans. I identified the commonest form as *L. corrugatus* and included my specimens from Port Stanley. Neither living animals nor sections showed eyes. I was at this time searching for *Cerebratulus steinini* which Bürger had described in 1893 from more than twenty specimens collected at South Georgia. This species again possessed a few small eyes, but the description otherwise applied to *L. corrugatus*. Not being able to find any Heteronemertean with eyes, I came to the conclusion that certain organs that are apparent in sections of the head of *L. corrugatus* close to the inner ends of the cephalic slits had been mistaken for eyes, and I accordingly synonymised *C. steinini* with *L. corrugatus* (1934). These organs are, I believe, part of the nerve-supply to the cephalic slits and in life they appear as chalky-white granules.

This explanation covers the discrepancy in the account of *C. magalhaensicus*, and I assert that although *L. corrugatus* varies greatly in colour, size, and shape, it never possesses eyes.

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The seasons in a tropical rain-forest (New Hebrides). Part 5. Birds (*Pachycephala*).

By JOHN R. BAKER, D.Sc., A. J. MARSHALL, and T. H. HARRISSON. (Communicated by Prof. E. S. GOODRICH, F.R.S., F.L.S.) (From the Department of Zoology and Comparative Anatomy, Oxford.)

(With 3 Text-figures and PLATE 1)

[Read 11 April 1940.]

INTRODUCTION.

The island of Espiritu Santo, New Hebrides (Pacific Ocean), was chosen for a special study of the biology of the seasons because it presents a remarkably unvarying climate. In the tropics it is usual for there to be sharply marked wet and dry seasons, but in the northern New Hebrides there is no proper dry season. The proximity to the equator (15° S.) and the surrounding ocean ensure that seasonal changes in temperature are very small. It was the main object of the Oxford University Expedition of 1933–4 to investigate seasonal phenomena in animals and plants in this remarkably unseasonal climate. Previous communications in this series have dealt with meteorology (Baker and Harrisson, 1936), botany (Baker and I. Baker, 1936), fruit-bats (Baker and Z. Baker, 1936) and insectivorous bats (Baker and Bird, 1936).

We wish to acknowledge our indebtedness to those organizations which supported the Expedition, namely, the Royal Society, the Percy Sladen Trust and the Oxford University Exploration Club, and to express our thanks to Professor E. S. Goodrich, in whose Department the results of the Expedition's investigations are being worked out. We also acknowledge much help from the other members of the expedition, Miss I. Baker, Mrs. Z. Baker and Mr. T. F. Bird. Mr. N. B. Kinnear has kindly helped us by showing us the eggs of *Pachycephala* spp. in the British Museum (Natural History) and in other ways.

General remarks on Pachycephala pectoralis, *the species chosen for special study.*

Observations were made on the reproduction of many species of birds, and an account of our findings will be published later. This paper is concerned only with one genus and mostly with one species, which was chosen for concentrated study on account of the advantages which it presented. We required a non-migratory species, so that we could study it throughout the year in one place, and it was necessary that it should be abundant and easily obtained.

It was desirable also that it should live in the natural rain-forest, rather than in the native gardens, and also that it should be a species which lived for the most part in the shade of the forest, below the leaf-canopy, for then the environmental conditions to which it was subjected would be accurately measured by our forest meteorological station. It was further required that the chosen species should not nest in inaccessible places and that the nest should be fairly easily found. An added advantage would be that adults could be sharply distinguished from young birds by a simple criterion.

All the advantages are presented by our chosen species, the Golden Whistler, *Pachycephala pectoralis* (Latham), which is illustrated in Pl. 1. *Pachycephala* is a genus of Passerine birds, thought to be allied to the shrikes or to the flycatchers. *P. pectoralis* was first described by Latham in 1801. It is a small bird, the males weighing (in the New Hebrides) some 28 gm. and the females about 4 gm. less. The male is olive-green above and has a black crown, a white throat, and a brilliant gamboge-yellow under-surface. The white and yellow are sharply separated by a black pectoral stripe, to which the specific name refers (see Latham, 1801). A good coloured figure is given by Froggatt (1921), who, like many authors, uses the name *P. gutturalis*. The female lacks the brilliant coloration of her mate, and is mostly greyish brown with a dull greyish-white chin and throat. The male has a striking song, which is one of the most familiar sounds of the New Hebridean rain-forest. A single loud note is repeated a number of times and then there is a final higher note, closely resembling the resounding crack of a whip.

Pachycephala pectoralis has a very wide distribution. It occurs right across Australia from the extreme west (including Rottnest Is.) to the east coast and beyond to Lord Howe Island. It occurs also in Tasmania, which is its southernmost limit. In the north it is found from the eastern part of Java, eastwards through Sumbawa and Flores (where it was found by A. R. Wallace) to the Moluccas and New Guinea, and thence through New Britain and the Solomon Is. to the New Hebrides, New Caledonia, and Fiji (Alexander, 1921 ; Hartert, 1928 ; Mayr, 1932 *a* and 1932 *b* ; Rensch, 1931 ; Wallace, 1863). It covers a vertical range from sea-level to 1200 metres in the East Indies (Rensch, 1931). For the most part the Golden Whistler is a woodland bird, though it is stated to invade the suburban gardens of Sydney in winter (Le Souëf, 1920).

P. pectoralis is essentially a non-migratory species and the whole life of each individual is usually spent in one locality (Chisholm, 1938 ; Howe, 1932 ; etc. ; but see Agnew, 1921, for a small exception). It is probably on account of its non-migratory habits that the species has no fewer than 70 geographical forms, a number which easily exceeds that of any other species of bird (Mayr, 1932 *a*). In the New Hebrides and Banks Is. the races of the various islands have indistinguishable or very similar males, while the females are distinct (Mayr, 1932 *b*).

All observers agree that *P. pectoralis* is insectivorous (Cleland, 1910 and 1911, Lea and Gray, 1935). Orthoptera, Rhynchota, Coleoptera, and Lepidopterous and Hymenopterous larvæ are stated to be the usual food. Sometimes spiders are found in the stomach and occasionally small seeds. In the New Hebrides we found the stomach-contents to be mostly beetles and Orthoptera Saltatoria, with seeds from time to time and occasionally an earwig, a cicada or other Rhynchotan, a Lepidopterous larva, or a spider. Other miscellaneous objects which we found in stomachs were a gecko (*Lepidodactylus lugubris*), five inches long, chillis, a seedling, and a leaf.

The nest, generally situated some 5–12 feet from the ground, is a rather rough, open cup-shaped structure (see North, 1906–09), built by the female alone (Howe, 1928). An excellent photograph of the nest and eggs is given by Jackson (1921). The eggs are commonly two or three in number. The colour of the background is creamy to pale buff, and there are freckles of umber-brown, especially in a zone running round the egg near its broader end.

The eggs are laid each day until the clutch is complete. Incubation is shared by both sexes (Howe, 1928). The young hatch 16 days after the last egg was laid and leave the nest 11 days after hatching (observations in Victoria by Hall, 1900). In New South Wales there are two or more broods in the season (North).

It is very easy to distinguish the young of both sexes from adults, because the young have reddish brown in the tail-coverts and elsewhere, which is completely lacking in mature birds. The period of maturity is prolonged and it is not until the second year that the full plumage of the adult male is assumed (Gould, 1865). There is not a seasonal change in the kind of plumage.

A number of authors report that the males sing and perhaps breed in immature plumage (Howe, 1928; Lawson, 1905; Mathews, 1920; Whitlock, 1922), but it is possible that this is a mistake. Our own dissections of a large number of males in immature plumage (rufous tail-coverts, etc.) showed undeveloped testes. A very curious circumstance, however, is that *adult* males sometimes possess *adult female* plumage, and we found that these sometimes had large testes. For a discussion of this subject, see Mayr, 1932 *a* and 1934. We have omitted these anomalous specimens from consideration in this paper when calculating the mean weight of the testes, the percentage of males fecund, etc.

Observations on the breeding-season of Pachycephala pectoralis *in the New Hebrides*, 1933–4.

Specimens were shot monthly from September 1933 to August 1934 inclusive in the rain-forest of Hog Harbour, Espiritu Santo, New Hebrides (15° S.). So far as possible the shooting of specimens took place between the 10th and 20th of each month. A considerable number of immature birds was shot, since it is difficult to distinguish them from adult females until one has them in one's hands. Adults were distinguished from young by the criteria mentioned above.

The number of adults dissected is shown in Table I (in which adult males in adult female plumage are omitted).

TABLE I.—The number of adults dissected.

	Adult males dissected.	Adult females dissected.
September	16	8
October	15	15
November	15	15
December	14	15
January	16	16
February	18	15
March	11	12
April	14	14
May	15	14
June	16	11
July	12	5
August	9	8
	171	148

The adult males were treated as follows. The testes were dissected out and either weighed fresh or preserved in formol-saline-alcohol and weighed subsequently. The two testes were weighed together to the nearest 10 milligrams. When the testes were weighed after preservation, an addition of 10 per cent. was found to be necessary to correct for the loss of weight caused by the preservative. The results are shown in Table II.

TABLE II.—Weights of both testes of adult males throughout the year, in milligrams.

September. (Fresh weights.) 1000, 390, 790, 490, 740, 760, 870, 830, 610, 690, 460, 620, 1050, 770, 780, 490. Mean weight, 709.

October. (Fresh weights.) 550, 530, 460, 920, 890, 900, 220, 660, 1040, 1200, 630, 880, 720, 300, 340. Mean weight, 683.

November. (Fresh weights.) 250, 900, 1100, 450, 800, 700, 90, 80, 540, 180, 20, 270, 10, 30. Mean weight, 387.

December. (Fresh weights.) 0, 10, 10, 10, 10, 0, 20, 0, 70, 20, 80, 10, 20, 10. Mean weight, 19.

January. (Fresh weights.) 70, 80, 150, 80, 70, 160, 40, 260, 40, 90, 20, 40, 10, 50, 40. Mean weight, 80.

February. (Preserved weights.) 610, 120, 10, 100, 30, 110, 10, 70, 100, 310, 140, 50, 470, 110, 220, 120, 70, 20. Mean weight, corrected to allow for loss of weight on preservation, 163.

March. (Preserved weights.) 140, 70, 440, 450, 120, 80, 90, 650, 60, 330. Mean weight, corrected, 267.

April. (Preserved weights.) 240, 170, 240, 240, 340, 320, 80, 530, 520, 240, 390, 490, 540, 540. Mean weight, corrected, 384.

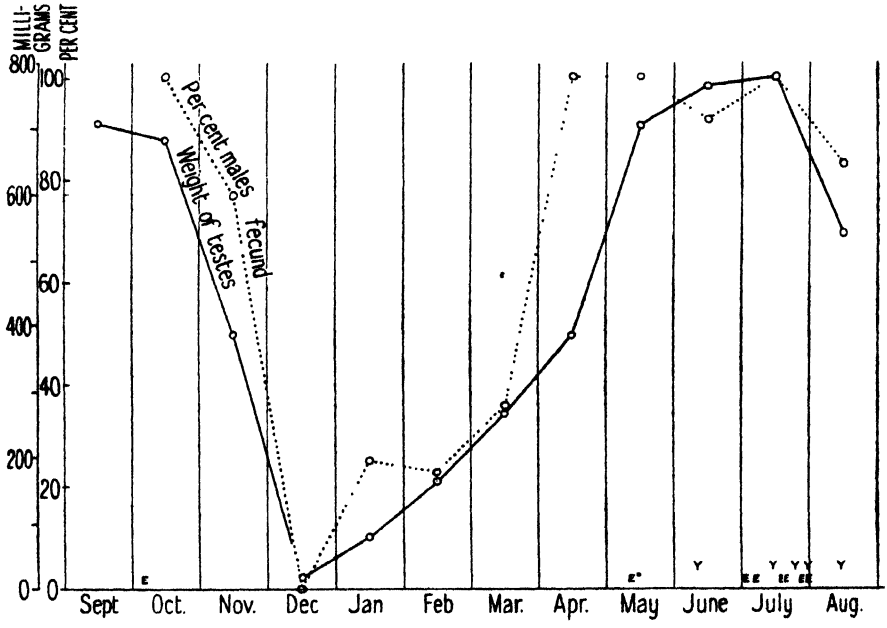
May. (Preserved weights.) 240, 770, 660, 730, 540, 600, 470, 800, 450, 910, 600, 690, 640, 720, 770. Mean weight, corrected, 703.

June. (Preserved weights.) 1100, 420, 1340, 770, 600, 970, 340, 550, 860, 700, 950, 350, 700, 720, 620, 130. Mean weight, corrected, 764.

July. (Preserved weights.) 370, 640, 720, 300, 660, 820, 770, 1050, 1030. Mean weight, corrected, 778.

August. (Preserved weights.) 210, 670, 370, 720, 210, 1030, 430, 290. Mean weight, corrected, 540.

The abundance of spermatozoa was determined either by teasing a fragment of fresh testis in saline and examining at once under the microscope or else by



TEXT-FIG. 1.—Graph showing the reproductive cycle in *Pachycephala pectoralis* during the year 1933–4 at Hog Harbour, New Hebrides.

E = eggs found in nests. E° = egg found in oviduct. Y = young found in nests.

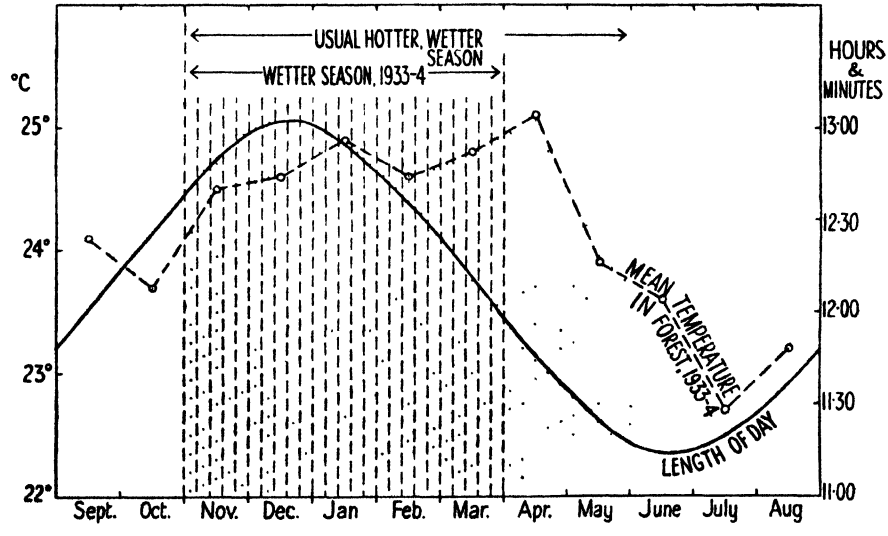
examination of microscopical sections of preserved material. The following symbols were used to indicate grades of abundance of spermatozoa :—

3. Full normal abundance.
2. Numerous, but noticeably less than full normal abundance.
1. Few, so that it takes some trouble to find any.
0. No spermatozoon seen.

The results are shown in Table III. (In a few cases the sperm-abundanec was recorded, but the testes not weighed, and sometimes the reverse occurred. This accounts for the apparent discrepancies between Tables I, II, and III.) When the sperm-abundance is 3, the bird is regarded as fecund ; if 2, 1, or 0, it is regarded as non-fecund.

TABLE III.—The number of adult males showing the different degrees of sperm abundance throughout the year (except September).

	Total no. examined for abundance of sperms.	No. showing the different degrees of sperm abundance.			
		3.	2.	1.	0.
October 1933	15	15	—	—	—
November	13	10	—	—	3
December	14	—	1	2	11
January 1934	16	4	4	4	4
February	13	3	3	1	6
March	11	4	2	3	2
April	3	3	—	—	—
May	12	12	—	—	—
June	13	12	1	—	—
July	11	11	—	—	—
August	6	5	1	—	—



TEXT-FIG. 2.—Graph showing seasonal changes in the physical environment at Hog Harbour, New Hebrides.

Tables II and III are represented graphically in text-fig. 1, which shows the variations in the mean weight of both testes and in fecundity of males throughout the year. The striking fact which emerges from a study of text-fig. 1 is that there is an enormous seasonal change in the weight of the testes. At the height of the breeding-season, in June and July, the testes (both together) average about 770 milligrams: in December they average 19. Thus at one time of year the testes weight more than 40 times as much as at another; and in this exceptionally unvarying climate the testicular changes are comparable with those of birds inhabiting the northern parts of Europe, where seasonal changes in climate are very great. One may say that the testes are large and the fecundity high from April till October, while the extreme non-breeding condition occurs in December.

The histological changes in the testes are as great as the variation in weight would lead one to suppose. Pl. 1 shows a section of a February testis, at the time when the very first signs of recrudescence are appearing (Pl. 1, fig. 2), and also one taken in May, during the breeding-season (Pl. 1, fig. 3). The two sections are shown at the same magnification. In the May testis one sees a big tubule containing large numbers of spermatozoa arranged in clumps. In the February testis the tubules are very small, and there is not a spermatozoon to be seen—indeed, there is no later stage in spermatogenesis than primary spermatocytes in synizesis, and the majority of the cells are spermatogonia. The bird from which this testis was taken was, of course, an adult male in full male plumage.

In the female the seasonal changes in the gonad are not so striking, except that when one happens to kill a bird which is about to lay, very large oocytes are, of course, found. A bird taken on 11th May had an oocyte 10 mm. in diameter in the ovary and an egg in the oviduct. In every female dissected the length of the ovary and the diameter of the largest oocyte was measured to the nearest quarter of a millimetre. The length of the ovary was not found to vary significantly during the year, as these figures from the height of the breeding season (June–August) and the reverse (December–January) will show:—

December ..	7, 7, 7, 6¼, 6¼, 6, 5½, 5, 5, 4¾, 4½, 4, 4, 4.
January ...	9½, 9, 8, 7, 7, 6¾, 6¾, 6½, 6¼, 6, 6, 6, 5, 5, 4¾, 4½.
June	10, 8, 7, 6, 5½, 5½, 5, 5, 4½, 4½, 3½.
July	8, 7½, 6, 6, 5.
August	13, 8, 8, 7, 7, 7, 6, 5.

The largest oocyte in the ovary is always small in the non-breeding-season, its most usual diameter being ¾–1 mm. In the breeding-season the most usual diameter for the largest oocyte is 1¼–1½ mm. (i.e. about eight times the volume). The size of the largest oocyte in each month of the year is shown in Table IV.

Search was made for nests and eggs. All the eggs listed below were living, addled ones being disregarded.

Nests containing unincubated eggs were found on July 2, 18, 27, 27.

TABLE IV.—The number of adult females whose largest oocytes are of various diameters : data for each month of the year.

	Diameter of largest oocyte (mm.).				
	½ and less.	¾-1.	1¼–1½.	1¾–2.	2¼ and more.
September	—	2	2	4	—
October	3	4	4	4	—
November	3	5	5	2	—
December	2	11	2	—	—
January	1	13	1	—	—
February	1	7	6	1	—
March	—	4	5	3	—
April	1	3	8	2	—
May	2	6	3	1	2
June	2	3	5	—	1
July	—	—	4	1	—
August	—	2	3	1	2

Nests containing partly incubated eggs were found on July 7, 19.

Nests containing living eggs (condition as regards incubation not recorded) were found on Oct. 5 ; July 30, 30, 30, 30, 30, 30, 30, 30.

Nests containing young were found on June 11 ; July 14, 24, 24, 30 ; Aug. 14.

In accordance with the previously published notation (Baker, 1938 *a*, 1938 *b* : see also Appendix to this paper), the egg-season may be given as v^2–VII^1–$VIII^1$–x^1. The reproductive season is as sharply delimited as in birds of temperate regions. We have no means of knowing whether the egg-season is approximately the same every year, but the evidence from a study of moulting, given below, would suggest this.

We have records of having obtained specimens in immature plumage in every month of the year except March. The absence of records from March is of no significance, since we got 19 juveniles in February and 17 in April. There is no evidence of juveniles being particularly abundant at any season. In this species, in which a year is spent in immature plumage, nothing can be discovered about the breeding-season by enumerating the number of young collected in different months. Meyer (58) indicates that in the island of Vuatom, New Britain, most young are seen from March to September, but it is legitimate to question whether this observation throws any light on the breeding-season there. Meyer does not give any of the data upon which he bases his statement as to the breeding-season of *P. pectoralis* in Vuatom.

Moult.—Many of our birds of both sexes were examined for moult. The results, which are shown in Table V, are clear-cut : the moulting-season is

September to December, but feather-replacement goes on sporadically throughout the year. Of eleven birds studied for moult in December, ten were in full moult. The species moults, like the birds of temperate regions, when it has finished breeding. The moulting-season agrees roughly with what Mayr had found as a result of the study of skins of *P. pectoralis* taken in the northern New Hebrides by the Whitney South Sea Expedition seven years before (1926–7). Mayr (1932 *b*) reports that the specimens collected in January are in full moult, while November is shortly before the moulting period. Thus the evidence derived from moult suggests that the reproductive season occurs at approximately annual intervals.

TABLE V.—Feather conditions in adults of both sexes during the year.

	Moulting.				Total no. not moulting.
	No. in full moult.	No. moulting, but amount of moult not noted.	No. showing patches of moult only.	Total no. moulting.	
September 1933 .	—	17	—	17	19
October ..	—	—	—	—	—
November ..	—	32	—	32	2
December ..	10	—	—	10	1
January 1934 ..	—	—	—	—	—
February ..	1	—	4	5	4
March ..	—	—	4	4	7
April ..	—	—	—	—	—
May ..	—	—	2	2	10
June ..	—	—	7	7	4
July ..	1	—	1	2	8
August ..	—	—	5	5	24
September ..	—	1	—	1	4

Changes in the environment during the year.—It will be remembered that the northern New Hebrides were selected for the whole of this investigation on account of the smallness of the changes in the physical environment during the year. The climate is always hot and wet, though usually a little hotter and considerably wetter from November to May. The year of our observations conformed to the usual conditions except that the wetter season lasted only from November to March (see Baker and Harrisson, 1936, for a full account of the meteorology). Thermometers in a Stevenson screen in the open showed the hottest month to have a mean temperature only 2°·1 C. (3°·8 F.) higher than the coolest. The thermometers exposed in a screen in the forest in which the bird lives gave the mean temperatures which are shown in text-fig. 2.

A comparison of this text-figure with text-fig. 1 shows that the growth of the testes takes place while the days are shortening and the rain abating; the egg-season occurs during the cooler, less wet season when the days are at their shortest or thereabouts. The meteorological data do not provide any obvious clue to the proximate cause of the breeding-season.

It might be thought that diet controls reproduction, but there is nothing in our studies to support such a view. When reproduction is at a standstill in January, and again at the height of the breeding-season in July, the food consists mainly of beetles and Orthoptera, with occasional seeds.

The only fact which emerges with complete certainty from a consideration of the environmental changes is that increase in length of day is not the cause of the breeding-season.

The breeding-seasons of Pachycephala *spp. throughout the range of the genus.*

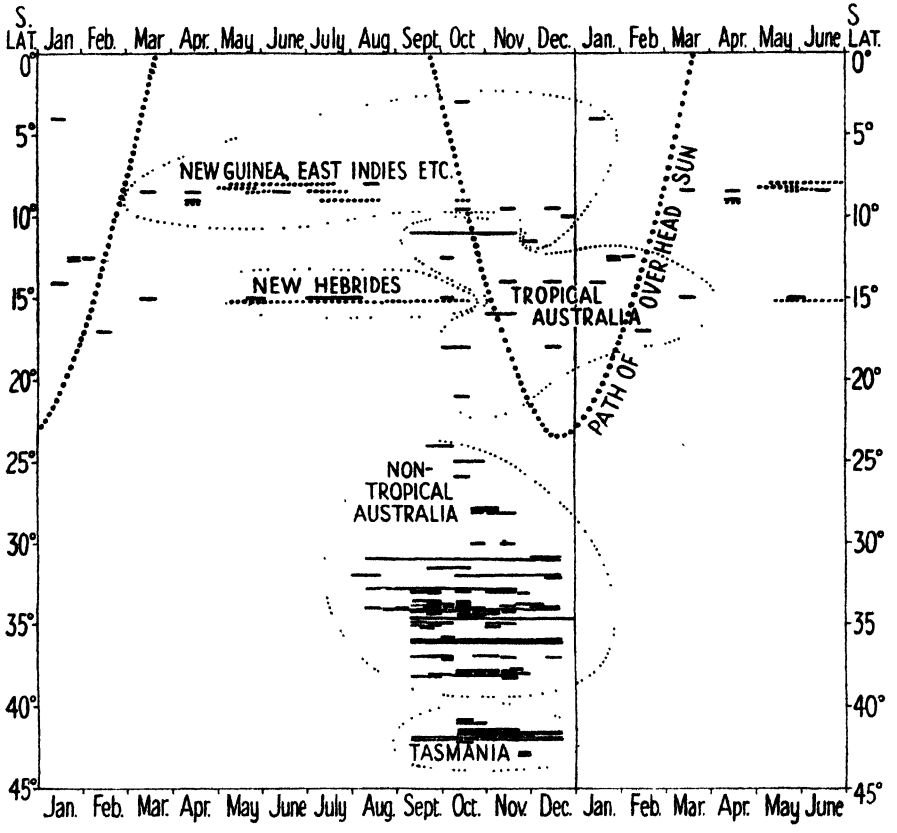
Our studies of *P. pectoralis* in the northern New Hebrides must be considered in relation to what is known of the breeding-seasons of the genus in other parts of the world. It is not very easy to amass the data necessary for a statement of the egg-season of any bird in any part of the world. Books of natural history usually give dogmatic statements, which are copied by authors, and the facts upon which the statements are based are not readily accessible. If the study of breeding-seasons is to become truly scientific, it is necessary to produce objective evidence of the breeding-season, and the best evidence is the actual finding of living eggs in nests. The data for the genus *Pachycephala* are given in the Appendix. With each record is given the latitude of the place where the observation was made.

The data given in the Appendix are represented graphically in text-fig. 3, which also shows (in a bold dotted line) the latitude of the places where the sun is directly overhead at mid-day. The horizontal lines show the recorded egg-seasons, while the horizontal rows of small circles indicate swollen testes.

Certain general conclusions stand out from the text-figure. In non-tropical Australia the egg-season is August to December, but especially September to November. Further south, in Tasmania, the egg-season does not start before September. In tropical Australia the season is definitely *later* than in the non-tropical parts. It extends from September to March, and is coincident with the time that the sun is approximately overhead at mid-day.

The difference between the egg-season of *Pachycephala* in the New Hebrides on the one hand and in similar latitudes in Australia on the other is most striking. In the New Hebrides the height of the egg-season occurs when the sun is lowest in the sky, over the Tropic of Cancer: in tropical Australia it is coincident with the overhead sun. Whatever may control the egg-season in this bird within the tropics, it is not length of day nor the position of the sun. Rainfall is not an explanation, for the height of the egg-season is reached in the wet season in tropical Australia and in the less wet season in the New Hebrides.

In New Guinea and the East Indies the egg-season shown by the genus is extensive, and it is difficult to define a start to it. There are records of eggs or swollen testes from all months except September and February. The data suggest that there may be two seasons in the year, one starting rather earlier



TEXT-FIG. 3.—Graph showing the egg-season (horizontal lines) and the season when the testes are swollen (horizontal rows of small circles) in *Pachycephala* spp. throughout the range of the genus. A ring of small dots is put all round the data from each area (tropical Australia, non-tropical Australia, etc.). The data on which the graph is based are given in the Appendix. The path of the overhead mid-day sun is shown by the bold dotted line.

than the New Hebridean season, and the other at the same time as the tropical Australian season. Two egg-seasons in the year are quite common in tropical birds (see Baker, 1938 *b*). No conclusion can be reached about the breeding behaviour of the genus in New Guinea and the East Indies until an intensive study of it has been undertaken there.

Discussion.

Previous reports in this series (Baker and Z. Baker, 1936 ; Baker and Bird, 1938) have shown that the mammals chosen for special study, a fruit-bat and an insectivorous bat, have sharp breeding-seasons despite the very small temperature changes during the year and the fact that there is no dry season. (It may be recalled that, on the average of many years, the least wet month in the place of observation has about twice as much rain as the wettest month over most parts of England.) The present paper shows that the selected Passerine bird, *Pachycephala pectoralis*, is also markedly seasonal in its reproduction. The onset of breeding is not so dramatically abrupt as in the insectivorous bat, but the seasonal change in the size of the testes is far greater. That the testes of a bird living in one of the most equable climates in the world should be forty times larger at one season of the year than at another is very remarkable. In both the bats the testes change much less in size during the year, and the fruit-bat (but not the Vespertilionid) keeps its epididymides full of spermatozoa throughout the year, although the season of copulation is short.

In one respect the environment is necessarily not so constant as in the equatorial rain-forest regions : the longest day is about $1\frac{3}{4}$ hour longer than the shortest. Nevertheless, it is scarcely possible that this is the controlling proximate cause of reproduction in *Pachycephala*, for in similar latitudes of Australia the reproduction is at its maximum when it is at its minimum in the New Hebrides, and vice versa. In the New Hebrides the growth of the testes and the onset of the egg-season occur when the days are getting shorter.

If the breeding-season is annual, as the moult-data given above would suggest, an internal rhythm cannot wholly control it (see Baker and I. Baker, 1936, pp. 517–8), though it may have an important effect. The environmental change which is the important proximate cause is still unknown to us. Experiment alone cannot decide the question, for there may be many artificial ways of starting and stopping reproduction in *Pachycephala*, which do not operate under natural conditions.

The work on *Pachycephala*, taken in conjunction with that on the bats, must dispel the notion that in the tropics the rule is for animals to breed all the year round or at irregular intervals. The more closely one investigates, the more surprisingly seasonal the behaviour of individual species is seen to be. There is, however, no special season when the young of most species of mammals and birds are appearing, corresponding to the spring and summer of temperate regions. Thus, for example, the eggs of *Pachycephala* are hatching especially about July and August, while the young insectivorous bats are born late in December. In the wet tropics all seasons are suitable for reproduction, but it would appear to be usual, among the higher Vertebrates at least, for each species to have a special breeding-season of its own.

Summary.

(1) In the remarkably unvarying tropical climate of the northern New Hebrides (Pacific Ocean), the Passerine bird *Pachycephala pectoralis* is as seasonal in its reproduction as are the birds of temperate climates.

(2) In the breeding-season the mean weight of the testes of adults rises to over forty times as much as in the non-breeding season.

(3) The growth of the testes and the start of the egg-season occur while the days are shortening.

(4) There is no seasonal change in diet.

(5) Moulting takes place after the end of the egg-season.

(6) The environmental change controlling the breeding-season is not known.

(7) The egg-season of *Pachycephala* spp. in the tropics of Australia comes at quite a different season of the year from that of *P. pectoralis* in approximately the same latitude in the New Hebrides.

Appendix.

Breeding records of Pachycephala *spp. throughout the range of the genus.*

In the column headed "eggs", the records are of actual finds of eggs in nests, except when the date is put in parentheses. The use of parentheses indicates that the time when eggs were in the nest was calculated from other breeding data (young in nest, etc.). In the "eggs" column the months are numbered in Roman numerals. Each month is divided into three parts, the 1st to the 10th, the 11th to the 20th, and the 21st to the end. These three parts are indicated by small Arabic numerals after the number of the month, thus :—X^1, X^2, X^3.

Place.	S. latitude.	Eggs.	Other breeding records.	Reference.
		Pachycephala pectoralis.		
New Britain	5	—	See p. 57 of this paper.	(58)
Dutch East Indies :				
Sumbawa	8	—	Swollen testes early to late May.	(63)
Flores	8½	—	Swollen testes early June, early to late July.	(63)
New Hebrides :				
Hog Harbour	15	(V^2–VI^1), VII^1–$VIII^1$, X^1	Swollen testes May–Oct.	This paper.
Queensland :				
Cardwell.....	18	—	"Breeding" Dec.	(9)
Macpherson Range...	28	X^3–XI^1	—	(23)

Place.	S. latitude.	Eggs.	Other breeding records.	Reference.
New South Wales :				
Place unspecified	--	VIII[3]	—	(60)
Ourimbah	33	XI[3]	—	(59)
Chatswood	34	X	—	(59)
,, ...	34	IX[3]	—	(59)
,, ...	34	X[3]–XI[1]	—	(59)
,, ...	34	(IX[2–3])	Newly hatched young 3rd Oct.	(59)
,, ...	34	(IX[3])	Young in nest 9th Oct.	(59)
Roseville	34	—	" Breeds freely " Sept.–Oct.	(59)
Chatsworth (?=Chatswood)	—	XI[3]	—	(21)
Eastwood.....	34	X[3]–XI[1]	—	(59)
Bundanoon	35	XI[1–2], XI[1]	—	(59)
Heathcote	34	X[3]	—	(59)
Sydney	34	—	General statement, eggs Sept.–Oct., a few till Dec.	(59)
Blue Mountains	34	—	General statement, eggs common Nov.	(59)
Victoria :				
Pine Plains	?	IX[3]	—	(33)
Mallacoota	38	—	" Nidification " seen mid. to late Nov.	(15)
Central N. Victoria ..	36 ?	—	" Nests " Sept.–Dec.	(43)
Heytesbury	38	IX[3]–XI[3]	—	(26)
Oakleigh	38	IX[2–3]	—	(21), (60)
Gippsland	38	XI[3]	—	(21), (60)
,, ...	38	X[3]–XI[1]	—	(51)
Tremont.....	38	X[3], XI[3]	—	(35)
Mitcham	38	XI[1]	—	(35)
Maryborough	37	(XII)	Young in nest early Jan.	(16)
West Australia :				
Lake Grace	33	—	General statement, nest is found Aug.–Nov.	(11)
Tasmania :				
Place unspecified	Ca. 42	—	General statement, " nests " Oct.-Dec.	(49)
,, ,, ...	Ca. 42	—	General statement, " breeding-season " Oct.–Dec.	(48)
Hobart	43	XI[3]	—	(22)
Evandale	42	—	General statement, eggs Oct.–Nov.	(59)
Circular Head	41	X[3]	—	(59)
Lord Howe Island	31½	IX[3]–X[3]	—	(52)

Place.	S. latitude.	Eggs.	Other breeding records.	Reference.
		PACHYCEPHALA ROBUSTA (=*P. pectoralis robusta*).		
Torres Strait :				
Darnley Is.	10	XII^3	—	(50), (51)
		PACHYCEPHALA MELANURA.		
Northern Territory :				
Daly River	14	I^2	—	(59)
Western Australia :				
Derby	17	II	—	(51)
		PACHYCEPHALA RUFIVENTRIS.		
Northern Territory :				
Coburg Peninsula ...	11	—	General statement, eggs Sept.–Nov.	(25)
Port Darwin	12½	X^1, I^3	—	(46)
Hermannsburg	24	IX^3–X^1	—	(70)
Queensland :				
Bloomfield River	16	XI^{1-2}	—	(44)
Richmond	21	X^2	—	(10)
Dawson River	25	X^{2-3}	—	(21), (60)
Cairns	26	X^3	—	(59)
New South Wales :				
Place unspecified	—	X	—	(21), (60)
Liverpool	34	X^{2-3}	—	(21), (60)
Sydney	34	(XII^{1-2})	Half-grown young in nest 21 Dec.	(31)
,, ...	34	—	General statement, eggs Sept. to end of Dec., especially Oct. to mid-Dec.	(59)
Barrington.....	32	XII	—	(37)
Canterbury	34	IX^3–X^1	—	(59)
Chatswood	34	X^1	—	(59)
Copmanhurst	30	X^3	—	(59)
Enfield	34	(XI^3–XII^1)	Nearly fledged young in nest 22nd Dec.	(59)
Roseville	34	IX^{2-3}	—	(21)
Dolroyd	?	X	—	(21)
Victoria :				
Central N. Victoria ..	36 ?	—	General statement, " nests " Sept.–Dec.	(43)
Mallacoota	38	—	" Nesting " mid. or late Nov.	(15)
South Australia :				
Lake Frome District .	31	—	" Breeds " Aug.–Dec.	(57)
,, ,, ,, .	31	XII^{1-2}	—	(69)
Eyre Peninsula	33	—	" Nests " found Oct.	(71)

Place.	S. latitude.	Eggs.	Other breeding records.	Reference.
Western Australia:				
Place unspecified	—	X^1	—	(21), (60)
Derby	17	—	Building nest 1st Aug.	(27)
Northam District ...	32	—	General statement, "breeding-season" extends Oct.–Dec.	(39)
Broome Hill	34	X^2	—	(51)
" "	34	X^2	—	(13)
Napier Broome Bay..	14	XI, XII	—	(30)
	PACHYCEPHALA RUFOGULARIS.			
Victoria:				
Mallee.....	Ca. 35	IX^{2-3}	—	(62)
South Australia:				
Pinnaroo	35	IX^3–X^1	—	(62)
	PACHYCEPHALA INORNATA.			
Queensland:				
Cardwell.....	18	X^1, X^2	—	(68)
New South Wales:				
Kilfera	33	XI^{1-2}	—	(59)
Victoria:				
Maryborough	37	IX^2, IX^3–X^1, X^1	—	(16), (51)
Hawk Plain, Carina .	35	—	"Nesting" mid-Sept.	(32)
Murrayville	35	IX^2 or 3	—	(30)
Wimmera.....	36	X^1	—	(59)
Bendigo	37	XI^2	—	(20)
St. Arnaud	37	X^3–XI^1	—	(61)
South Australia:				
Euro Bluff	?	X	—	(59)
Eyre's Peninsula ...	33	IX^{2-3}, IX^3	—	(62)
Gawler Ranges	32	$VIII^{1-2}$	—	(62)
Western Australia:				
Interior, place unspecified	—	($VIII^1$)	Newly hatched mid-Aug.	(25)
Broome Hill	34	$VIII^2$	—	(13), (12)
	PACHYCEPHALA LANIOIDES.			
Northern Territory:				
Roper River	15	(III^2)	Young in two nests 29th March.	(67)

Place.	S. latitude.	Eggs.	Other breeding records.	Reference.
		PACHYCEPHALA OLIVACEA.		
Queensland :				
Macpherson Range...	28	X^3, X^3–XI^1, XI^{1-2}	—	(38), (69)
New South Wales :				
New England District	30	XI	—	(59)
Victoria :				
Gippsland	38	X	—	(59)
Tasmania :				
Place unspecified	Ca. 42	—	General statement, " breeding-season " Sept.–Dec.	(48)
,, ,, ...	Ca. 42	—	General statement, " nests " Sept.–Dec.	(49)
,, ,, ...	Ca. 42	—	Eggs generally found Oct.	(59)
Mount Bischoff	41	X^{2-3}	—	(59)
Evandale	42	—	" Nests " have been found 24th Oct.–2nd Dec.	(59)
Hobart	43	XI^2	—	(22)
		PACHYCEPHALA SIMPLEX.		
Northern Territory :				
Place unspecified	—	(I–II)	Female with large eggs in ovary and incubation patch 3rd Feb.	(14)
Port Darwin	12½	I^2, II^1	—	(45)
		PACHYCEPHALA GRISEICEPS.		
S.E. & S. New Guinea..	Ca. 9	(IV)	Jan. & Feb., no enlarged gonads. Apr., female in laying condition, males have enlarged testes. Oct., males still have enlarged testes, females not in laying condition. Dec., moulting, no enlarged gonads.	(56)

Place.	S. latitude.	Eggs.	Other breeding records.	Reference.
		PACHYCEPHALA MODESTA.		
New Guinea :				
Mt. Tafa	8½	—	Male taken 23rd May had enlarged testes, but was moulting.	(56)
		PACHYCEPHALA RUFINUCHA.		
New Guinea :				
Mt. Tafa	8½	(IV)	Nestling not long out of nest, 12th May. No enlarged gonads May, Aug., Sept.	(56)
		PACHYCEPHALA LEUCOSTIGMA.		
New Guinea :				
Snow Mts.....	4	(Ca. 1)	Very young bird, just from nest, Jan. or Feb.	(65)
		PACHYCEPHALA SOROR.		
New Guinea :				
Deva Deva, Mafulu ..	8½	- -	May, no moulting Moulting specimens taken Sept.–Nov.	(56)
Doriwaida	?	VIII	—	(21)
		PACHYCEPHALA SCHEGELII.		
S.E. & S. New Guinea..	Ca. 9	—	Enlarged testes July–Aug.	(56)
		PACHYCEPHALA GRISEONOTA.		
Dutch E. Indies :				
Ceram.....	3	X	—	(21)
		PACHYCEPHALA NUDIGULA.		
Dutch E. Indies :				
Sumbawa	8	—	Enlarged testes May–July.	(63)
		PACHYCEPHALA FORTIS.		
Trobriand Is.	8½	III, VI	—	(64)
New Guinea :				
Fergusson Is.	9½	X, XI, XII	—	(64)
		PACHYCEPHALA ROSSELIANA.		
Louisiade Archipelago .	11½	XI and/or XII	—	(28)

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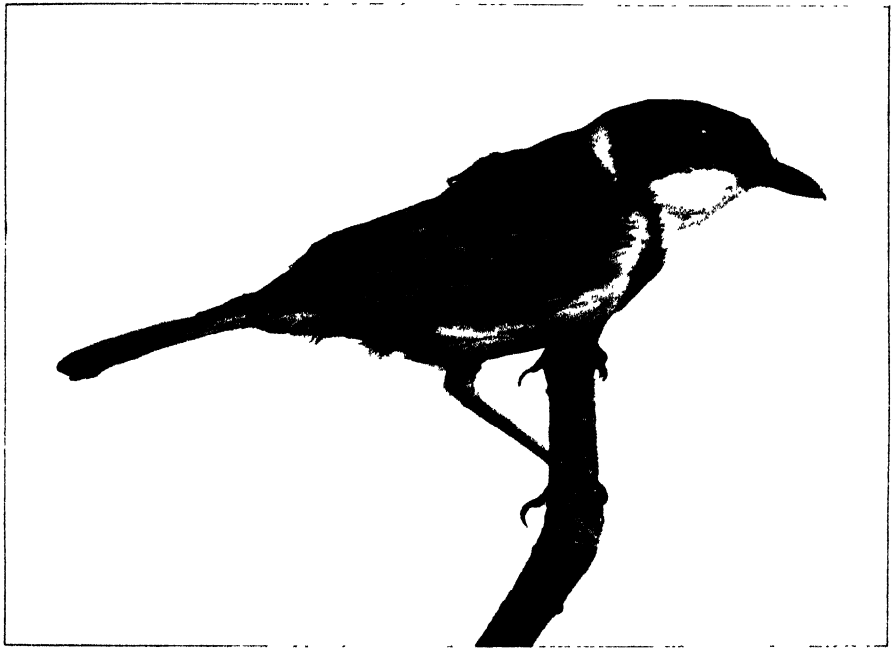
EXPLANATION OF PLATE 1.

Fig. 1. *Pachycephala pectoralis*: an adult male from the New Hebrides.
Fig. 2. A section through part of the testis of an adult male *P. pectoralis* in February. Iron haematoxylin.
Fig. 3. A section through part of the testis of an adult male *P. pectoralis* in May. Iron haematoxylin. The magnification is the same as in fig. 2.



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PACHYCEPHALA PECTORALIS (LATHAM).

Mabuia trivittata *, which belongs to the limbed, non-burrowing variety. In a preliminary study he showed that *Mabuia* is very similar to *Eumeces*, an account of the chondrocranium of which latter species was published by Rice (1920). As it has not been possible to continue the collaboration, I am completing the work on *Acontias meleagris*, using J. Dick's figures and preliminary account of *Mabuia trivittata* for comparison.

I wish to thank Professor Goodrich, of the Department of Zoology and Comparative Anatomy, Oxford, for his constant advice and encouragement; and Somerville College, Oxford, for a research grant which has made this work possible.

The chondrocranium of Acontias meleagris.

The late stage of *Acontias meleagris* available shows a chondrocranium largely ossified in the posterior region. Fig. 1 is a graphic reconstruction, lateral view, and fig. 2 is a ventral view of the olfactory and trabecular regions. The parachordal plate region is completely ossified and the basicranial fenestra and hypophysial fenestra are covered by the parasphenoid bone which is fused with the basisphenoid.

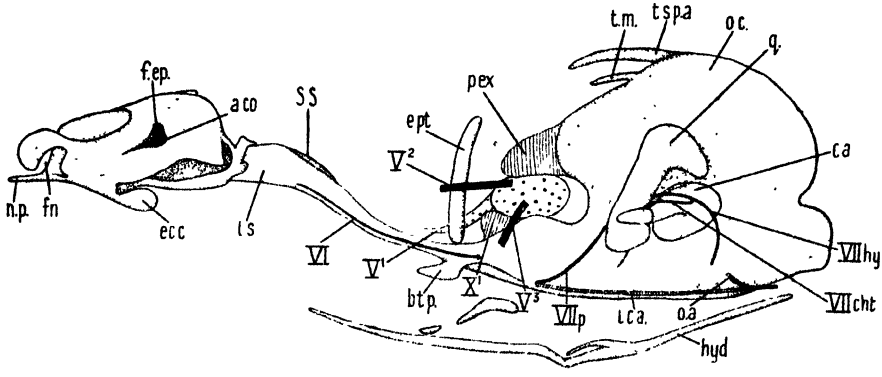


FIG. 1.—Chondrocranium of *Acontias meleagris*.

There is a single basioccipital condyle of the hypocentral type common to Squamata and Rhynchocephalia (see de Beer, 1929 & 1937); the notochord is still recognizable within the pleurocentral element fused to the anterior tip of the odontoid peg, and continuing forward dorsal to the basal plate and condyle.

There is a complete occipital arch with a tectum posterius.

The otic capsules, as in other skinks, are particularly large, and there is a tectum synoticum roofing the brain between them and continued forward in a long ascending process. The otic capsules are ossified. The prootic bone has a bony 'prootic extension' which forms part of the side-wall in the orbito-temporal region.

* Presumably the species now known as *capensis* Cuvier, the name *trivittata* being reserved for an Indian Skink. See Smith, Fauna Brit. India, II, Sauria, 1935, p. 276.—[ED.]

The columella auris is large, with a cartilaginous extracolumella inserted in the tympanic membrane, a boy shaft without processes, and a large foot-plate inserted in the fenestra ovalis of the otic capsule. The nerves and blood-vessels have the normal lacertilian relations to the columella auris (see fig. 1); i.e. the hyomandibular branch of the facial nerve runs back over the shaft of the columella auris, giving off a chorda tympani branch behind the shaft which runs forward again over the shaft and then down to the inner surface of the mandible. The internal carotid artery runs below the shaft and its orbital branch above it.

The orbitotemporal region is very incomplete. The skull is definitely tropitrabic, with a very long trabeculum communis dividing far back into paired trabeculae which carry large basitrabecular processes. At the stage of ossification represented in this embryo the cartilage of the paired trabeculae has been resorbed within the bony forceps of basisphenoid and parasphenoid. The latter covers the hypophysial fenestra, the posterior limit of which, the crista sellaris, appears to be unusually far behind the basitrabecular processes. The internal carotid artery, with the palatine branch of the facial nerve, enters the parabasal canal and immediately divides into two vessels, one of which penetrates the cranial cavity through the posterior corner of the hypophysial fenestra, and the other continues in the parabasal canal and runs forward to the orbit. Pearson (1921) describes the same branching and disposition of the carotid artery for *Lygosoma*.

All that remains of the side walls in the orbitotemporal region are small vestiges of the taenia marginales attached to the otic capsules. The interorbital septum is low and there are mere vestiges of supraseptal plates (see figs. 1 & 7).

The edge of the basal plate in front of the otic capsules is curved up to form a side wall in the region of the prootic incisure. In front of this is a bony plate in the line of the side wall which gives no indication of having been preformed in cartilage and which cannot represent a pila antotica, since the profundus nerve is medial and not lateral to it (see fig. 1, '*x*').

There is a large epipterygoid bone, supported on the pterygoid bone, in the line of the basitrabecular processes, and situated in the plane of the bony side wall of the skull (see fig. 3). It is very widely separated from the quadrate. It has the normal lacertilian relations with the branches of the trigeminal nerve, i.e. the profundus runs forward medially to the epipterygoid, whereas the maxillary and mandibular branches emerge from the cranial cavity behind the epipterygoid. The profundus is medial not only to the epipterygoid, but also to the membrane in which is forming the parietal downgrowths; it is located in a space between the dura mater and this membrane, and will be medial to the completed side wall.

The abducens nerve, after leaving the cranial cavity, runs forward below the profundus, but outside the cranial membrane. The sections are not very favourable for tracing the course of nerves, and I have not been able to detect

the oculomotor and trochlear nerves, nor to tell whether these nerves have an intramural course and emerge with the optic nerve through a foramen corresponding to the foramen orbitale magnum of the snake (de Beer, 1926). At any rate the abducens nerve has an independent course outside the intramural space occupied by the profundus.

The quadrate, which, as already mentioned, is widely separated from the epipterygoid, is freely articulated on a small parotic process; there is no intercalary cartilage intercalated between quadrate and parotic process.

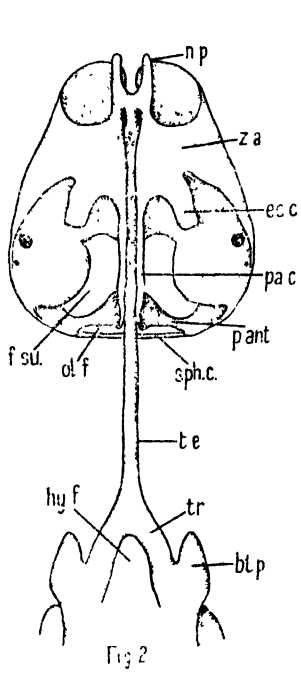


Fig 2

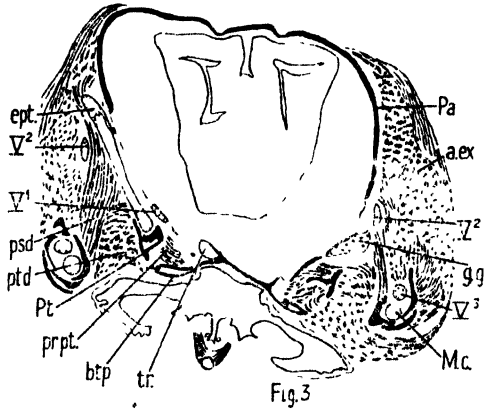


Fig.3

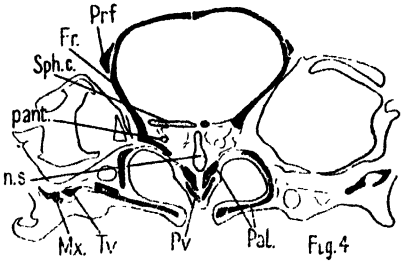


Fig.4

Fig. 2.—Olfactory and trabecular regions, ventral view.
Fig. 3.—Transverse section, *Acontias meleagris*, showing epipterygoid.
Fig. 4.—Transverse section, *Acontias meleagris*, showing back of olfactory region.

Between the basitrabecular process and the pterygoid bone there is no trace of a meniscus pterygoideus. From the arrangement of the constrictor dorsalis musculature there would appear to be a certain amount of movement at the basitrabecular pterygoid joint. There is a protractor pterygoideus from pterygoid to cranial floor, and in front of the epipterygoid there is a small levator pterygoideus, inserted on the front end of the pterygoid and attached to the cranial wall, which would ensure a certain amount of palatal movement. The epipterygoid, supported on the pterygoid and situated in the plane of the

cranial side wall, as already described, is ligamentously attached at its upper end to the cranial side wall, so that in this way movement of the pterygoid at the basitrabecular joint would be restricted.

The cartilaginous olfactory capsules are very complete, and correspond fairly closely to Rice's description for *Eumeces* and to J. Dick's findings for *Mabuia*. There are certain modifications due to the forward encroachment of a bony cranial cavity between the hind ends of the olfactory capsules. The sphenethmoidal cartilages are pushed forwards so that they run transversely from the posterior limit of the capsule roof to the nasal septum (see fig. 4) : they are immediately above the planum antorbitale (lamina orbitonasalis). This part of the nasal septum and olfactory capsule is restricted in height, being pressed below the bony cranial case. Anteriorly the nasal septum rises rapidly and the capsules rise to full height laterally outside the cranium. The roof of the olfactory capsules is incomplete, with large olfactory fenestrae and fenestrae superiores. On the other hand, the side wall is very complete, without a lateral fenestra ; there is a conchal infolding with an aditus conchae situated in a rather shallow depression between the posterior and anterior parts of the olfactory capsule. A foramen epiphaniale, for the exit of the lateral branch of the ethmoidal nerve, opens in this depression not far above the aditus conchae. The anterior cupola of the olfactory capsule is incomplete medially and the nasal septum is visible medially through the fenestra narina. Paired processes project from the ventral anterior margin of the nasal septum. The floor of the capsule is firm. Paraseptal cartilages run the whole length from the anterior medial margin of the planum antorbitale to a zona annularis which forms a wide floor beneath Jacobson's Organ, and an ectochoanal cartilage projects back from it.

The ossified skull.

Fig. 5 is a graphic reconstruction, lateral view, of the ossified skull of a late embryo, and shows clearly the adaptation to the burrowing habit. The anterior tip is solidly invested with bone : a stout premaxilla and a maxilla which forms an investing side wall to the ethmoidal region and overlaps the roofing nasals. The prefrontals complete the bony side wall outside the capsules, and medial to this side wall is another side wall formed by downgrowths of the frontals which enclose a cranial cavity which has pushed forward between the olfactory capsules and reduced the height of the nasal septum in this region. The eye is small and situated far forward outside this cranial box formed by the downgrowths of the frontals. The orbit is bounded by prefrontal, postfrontal and a tiny jugal which does not, at this stage, quite complete the postorbital arch between maxilla and postfrontal.

As already mentioned in the account of the chondrocranium, the interorbital septum is a low one ; it is pressed below the wide cranial cavity enclosed by downgrowths anteriorly of the frontals and continued behind these by similar downgrowths of the parietals. At the stage shown the parietal downgrowths

are incomplete ventrally and the side walls are partly membranous. The epipterygoid is situated in close contact with the parietal downgrowths and forms part of the side wall of the cranium.

The bony prootic extension, and the bony projection from the basal plate, in the region of the pila antotica, are in the plane off the membranous side wall. The trigeminal ganglion is situated between them, and the maxillary and mandibular nerves pass out over the latter bony plate. This orbitotemporal region of the cranium is unusually long, so that there is a wide gap between the postorbital arch and the temporal bones which are very much reduced. There

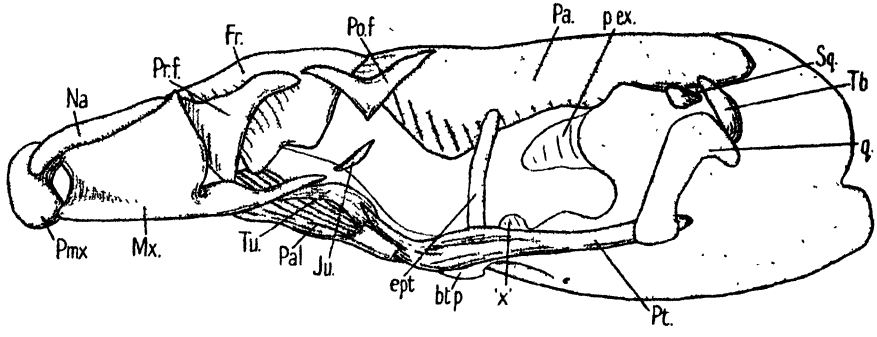


FIG. 5.—Skull of *Acontias meleagris* embryo ; graphic reconstruction.

are no temporal arcades or fossae. The squamosal is very tiny, and the tabular (supratemporal), situated behind it, wedged between the quadrate and the otic capsule wall, is larger than the squamosal. As would be expected from the small size of these temporal elements, the main attachment of the adductor externus muscles is to the cranial roof and side wall, but a few fibres appear to be attached both to the tabular and the squamosal *.

Figure 6 shows a very compact palatal floor to the solid anterior end of the skull. The premaxilla forms a wedge-like tip. A septomaxilla is present but

* Since this paper was written another one on the same subject by Prof. de Villiers has appeared in the *Anat. Anz. Jena*, LXXXVIII, 1939, pp. 320–47. There are some differences in the terminology used for some of the head bones. Prof. de Villiers, following Gaupp, regards the paraquadrate as distinct from the squamosal. In a paper entitled ' The Temporal Bone in Lizards, Birds and Mammal ' (*Anat. Anz. Jena*, LXXX, 1935, pp. 266–84) I have discussed Gaupp's theory, and agree with Thyng (1906) that ' there is no need for Gaupp's term " paraquadrate " for the Reptiles and Amphibia, since it is merely a synonym for squamosal, a bone which may be defined as a membrane bone primarily associated with the lateral surface of its quadrate ; with the migration of the quadrate (incus) into the tympanic cavity, the squamosal of the mammal secondarily becomes a bone of the otic capsule wall '. I therefore regard the outer of the two temporal bones in lizards as a squamosal, and the inner as a tabular (supratemporal). This terminology is that used by the great majority of morphologists to-day, de Villiers being the only notable exception who still accepts Gaupp's terminology.

does not show. The prevomers are paired and very large, extending laterally under the palatal plate of the maxillae; posteriorly they are overlapped by the palatal bones, which, too, are very large and are scroll-like—that is, they are rolled into a tube, open as a groove all along the ventral median line, and the tube contains an elongation of the nasal passage with the internal nares situated at the posterior end of the palatines. In this way the nasal passage is partially separated from the mouth passage (see fig. 7). The pterygoids are

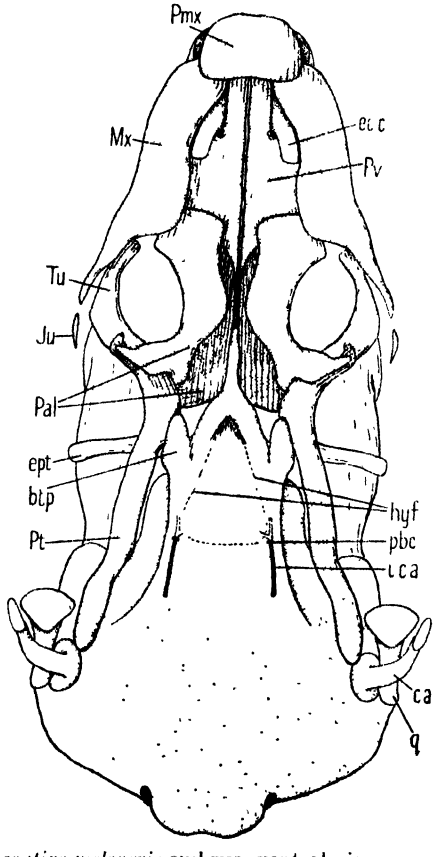
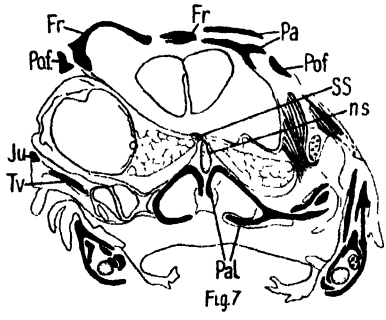
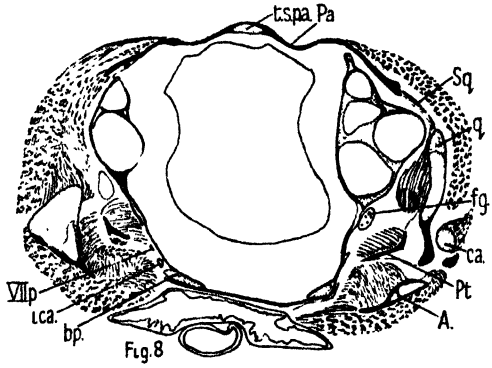


FIG. 6.—Skull of *Acontias meleagris* embryo, ventral view; graphic reconstruction.

strongly wedged in a posterior and lateral groove of the palatines; they are also supported by large transverse bones completing a ventral arch to the maxillae. The pterygoids, correlated with the elongation of the orbitotemporal region of the skull, are very long; as already described, they are supported on the large basitrabecular processes, and in turn support the epipterygoids. The free posterior ends lie close to the articular end of the quadrate, to the medial margin of which they are ligamentously attached.

The parachordal floor of the skull is fully ossified ; the parasphenoid is fused to the basisphenoid. Where the trabeculae diverge from one another, to form the hypophysial fenestra, they are held in forceps-like bony formations, the more ventral of which, extending laterally into the ossification of the basitrabecular process, is the parasphenoid. Behind the basitrabecular process the ventral parasphenoid and the dorsal basisphenoid form a parabasal canal in which runs the palatine branch of the facial nerve and one branch of the internal carotid artery ; another branch of this artery, as already described,





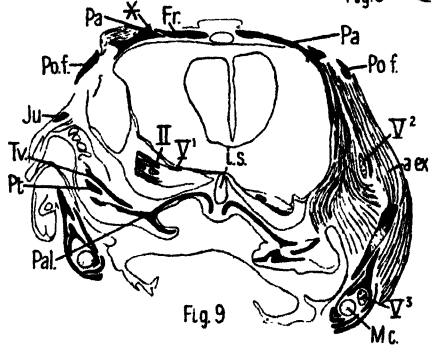


FIG. 7.—Transverse section, *Acontias meleagris*, showing tubular palatines.

FIG. 8.—Transverse section, *Acontias meleagris*, showing parietals fusing with ascending process of tectum synoticum.

FIG. 9.—Transverse section, *Acontias meleagris*, showing mesokinetic sliding contact * of frontals over parietals.

penetrates directly into the cranial cavity through the hindmost corner of the hypophysial fenestra and only occupies the hindmost part of the parabasal canal. Pearson (1921) describes this same disposition of the internal carotid artery in *Lygosoma*.

The problem of the nature of the kinetism of the skull in *Acontias* has necessitated careful work. The basitrabecular-pterygoid joint has already been

discussed. From the musculature it seems evident that there is a certain degree of movement at this joint. The normal lacertilian metakinetic skull has, in addition to the movable basitrabecular pterygoid joint, a sliding contact between the parietals and the underlying supraoccipital, so that the whole maxillary segment of the skull is movable upon the occipital segment. In the embryo stage of *Acontias* represented in the reconstructions, the parietals rest upon the ascending process of the tectum synoticum and upon the otic capsules. The parietal downgrowths in front of the otic capsules are not very extensive. A certain degree of movement might conceivably take place at this stage, but already there is indication of the parietals fusing with the ossifying processus ascendens (see fig. 8). In the macerated skull of the adult *Acontias* the parietals appear to be fused with the supraoccipital, and there could scarcely be any sliding between maxillary and occipital segments at this stage. The skull appears to conform to Versluys (1912) mesokinetic type—i.e. the frontals overlie the parietals and there could be a sliding contact there (see fig. 9). With the movement of the basitrabecular pterygoid joint a sliding movement would also take place at the frontal-parietal overlap, and the upper jaws, palate and nasal region would move relative to the cranial segment consisting of occipital and parietal regions. This type of kinetism Versluys calls mesokinetsim.

Comparison of Acontias *with other skinks.*

Rice (1920) has given a full account of the chondrocranium of *Eumeces*, and Pearson (1921) has described the skull of a late embryo of *Lygosoma*. As already mentioned, J. Dick has made reconstructions of the chondrocranium and skull of *Mabuia trivittata*, and written a preliminary account of this type which I use as a basis of comparison. *Eumeces* and *Mabuia* show a pretty typical lacertilian chondrocranium. The ossified skull also is a fairly typical lizard having the full complement of membrane bones, including a complete superior temporal arch of squamosal process meeting a process from the postfrontal. Both *Lygosoma* and *Mabuia* show a squamosal lying close to the parietal, so that at this stage there is no actual superior temporal fossa although the arch is complete.

The points of interest in comparing *Acontias meleagris* with the less specialized non-burrowing skinks are, firstly, the elongation of the orbitotemporal region, the disappearance of the chondrocranial side wall in this region, and the development of a membrane bone wall in its place from the downgrowths of the parietals, to complete which grow out also the bony prootic extension and the bony process from the margin of the basal plate; the epipterygoid assists also in the completion of this side wall to a complete cranial case. This cranial case is continued anteriorly by similar downgrowths of the frontals, which downgrowths account for the lowness of the interorbital septum, for the separation in the middle line of the orbits, and for the modification of the back of the olfactory capsules already described—i.e. the telescoping of the

sphenethmoidal commissures, the lowness of the nasal septum, and the medial separation of the back part of the capsules by the anterior extension of this cranial box.

The solidarity of the membrane bones surrounding the olfactory capsules, that is, the premaxillae, the maxillae, the nasals and the prevomers, gives a strong burrowing tip to the skull. This, with the smallness of the orbits, which do not project laterally but are contained within a space between the frontal downgrowths medially and the strong rim laterally of the postfrontal, prefrontal, maxilla and jugal, complete the picture of a strong, solid, but slender cranium without obvious protuberances which one would associate with a burrowing mode of life.

In keeping with this picture is the disappearance of the temporal arch; the postfrontal is well forward, at the front of the long orbitotemporal region, and both squamosal and tabular bones are reduced to small vestiges above the articulating head of the quadrate and in the occiput. The problem of the temporal bones and the identity of these bones in various Lacertilia has been dealt with by me in various papers (1932, 1935, and a paper on the chameleon now ready for publication). It will not be discussed again now, since the point at issue here is merely the reduction of the bones and the disappearance of the superior temporal arch which takes place independently in various Lacertilia, e.g. the geckos, *Typhlosaurus*, *Amphisbaena*, Anniellidae. In all except the geckos the disappearance of the superior temporal arch would seem to be, as in *Acontias meleagris*, an adaptation to the burrowing habit, with a smooth solid cranium. With the absence of temporal arcade the adductor externus muscles are attached to the wall and roof of the cranium.

Peters (1882), in his 'Reise nach Mosambique', figures the skull of an adult *Acontias niger* which has a complete superior temporal arch of postfrontal process meeting a process from the squamosal; there is as well a fair-sized tabular behind the squamosal. The loss of the temporal arcade in *Acontias meleagris* would be correlated with a greater adaptation to a subterranean existence. The body of *Acontias niger* is not as slender and snake-like as *Acontias meleagris*, and the former retains vestiges of hind limbs while the latter shows complete absence of limbs.

An interesting adaptation in the palate of *Acontias meleagris* has already been described, i.e. the medial dorsal plate of the palatine plate is extended and rolled over to form an almost closed tube with the more ventral plate of the same bone. In this palatine tube is enclosed an extension of the nasal passage, which is thus partially closed off from the mouth passage for quite a long distance. The Y-shaped palatine bone with dorsal and ventral arms projectinn above and below a dorsal groove of the mouth passage is observed in *Mabuia*, and may be a common feature of lizards, but the definitely tubular character of the palatine of *Acontias meleagris* I have not observed elsewhere. Pearson (1921) describes for the skink, *Lygosoma*, the same secondary palate, with naso-palatine groove almost shut off from the rest of the buccal cavity.

The condition of the pterygoid bone in *Acontias meleagris*—very long, lying close against the floor of the cranium, and supported by large basitrabecular processes—is in keeping with the rest of the skull adaptations. As already described, from the differentiation of the musculature, there must be a certain amount of movement at the pterygoid basitrabecular joint, but it would be fairly restricted by the attachment of the epipterygoid to the side wall of the skull.

The non-burrowing skinks, like Lacertilia generally, have metakinetic skulls. The transformation of the skull of the burrowing *Acontias* to the mesokinetic type already described has an interesting bearing on the affinities of lizards with snakes, but this will be discussed later.

Comparison with other burrowing lizards.

Peters (1882), in his 'Reise nach Mosambique', has given interesting figures of the skulls of various burrowing lizards and snakes. From his pictures of *Typhlosaurus aurantiacus* this degraded skinkoid (Anelytropidae) is very similar to my *Acontias meleagris*. In fact the whole account given above might apply also to *Typhlosaurus*, except that Peters figures only one vestigial temporal bone above the articulating head of the quadrate in *Typhlosaurus*. From its position above the articulating head of the quadrate, but overlapping the quadrate margin rather than being wedged between it and the otic capsule wall, it appears to be a squamosal. One would expect to find a tabular, vestigial at any rate, wedged behind the squamosal and situated in the occiput. But without the opportunity of observing serial sections of a skull it is not possible to say whether the absence of a tabular in Peter's *Typhlosaurus* is actual or due to the imperfection of the maceration method of preparation. My observations of lizard types in which the temporal bones tend to disappear (discussed 1935) have led me to expect that it is the squamosal which disappears first and the tabular which is retained. I would expect that serial sections of *Typhlosaurus* would reveal the presence of a small tabular behind the squamosal.

A comparison of *Acontias meleagris* with *Amphisbaena violacea* as figured by Peters reveals a number of very interesting points. The general morphology of the skull is similar, but even more slender and lacking in angles and projections calculated to impede a subterranean existence. The downgrowths of parietals and frontals have formed a solid cranial box extending to the skull floor and entirely obliterating the interorbital septum. The orbit is wedged in the angle of the maxilla and prefrontal, but there is no postorbital arch. There is no trace of an epipterygoid nor of any temporal arcade bones. Peters' figures do not reveal whether there is a 'prootic extension' helping to form the side wall of the cranium. The lower jaw is foreshortened and the quadrate relatively lengthened, which has the effect of lessening the gape of the jaws in a manner one might expect to be favourable to a burrowing mode of life. In palatal view, contrasted with the angular *Typhlosaurus*, the margin of maxilla, transversum and pterygoid is a smooth one. The prevomers are large.

The palatines seem to have a wide nasopalatine groove. The suborbital fenestra is narrow. The pterygoids are expanded laterally and seem to form part of a very flat cranial floor. In dorsal view, too, the width of the cranium in the orbitotemporal region is remarkable; there are neither orbital nor temporal vacuities.

Versluys (1912) pointed out that the Amphisbaenidae possessed mesokinetic skulls. With the downgrowth of the parietals to meet the basal plate and form a solid cranial case with the occipital segment the sliding contact between the parietals and the supraoccipital is lost, but is replaced by a more anterior sliding contact of parietals with frontals. This allows for a lifting of the nasal region, with the upper jaw and palate, relative to the solid cranial case; this Versluys called mesokinetism. We have already noted for *Acontias* a mesokinetism which contrasts interestingly with the metakinetism of the ordinary skinks.

Versluys reports, from a study of serial sections, that a basitrabecular process is lacking in *Amphisbaena*, but that a ridge is developed on the side wall of the skull base, and on this ridge the pterygoid is movably supported. The mobility of this pterygoid joint is confirmed by the presence of the appropriate muscles, especially the protractor pterygoidei. In another Amphisbaenid, *Trogonophis wiegmanni*, Versluys observed short basitrabecular processes, and this type also was mesokinetic.

Comparison with the Ophidia.

In addition to these skulls of various burrowing lizards Peters figures the skulls of the burrowing snakes, *Onychocephalus* (=*Typhlops*) and *Stenosoma* (*Glauconia*). In 1932 I gave graphic reconstructions of the skull of the burrowing snake *Leptotyphlops* (=*Glauconia*) *nigricans*. There is an interesting closeness of similarity between the skulls of *Glauconia* and *Amphisbaena*. Both have the solid cranial box formed by the downgrowths of parietals and frontals extending to the basis cranii and obliterating the interorbital septum. Both have the tiny orbit wedged behind the rim of the maxillae and prefrontal, separated medially by the downgrowths of the frontals, and lacking a posterior margin since both jugal and postfrontal are absent. The cranium is wide in the orbitotemporal region and there are no temporal vacuities nor temporal arcades. In *Glauconia nigricans* my serial sections revealed a minute temporal bone above the articulating head of the quadrate, wedged between it and the otic capsule wall, which I gave reasons for assuming to be a tabular and not a squamosal. The lower jaw in *Glauconia* is foreshortened as in *Amphisbaena*, but the quadrate is elongated. The burrowing tip of the Glauconid skull is less compact than in *Amphisbaena*; the maxillae do not form a side wall over the olfactory capsules and they project well out from the side of the cranium and have no transversum to support them posteriorly on the pterygoids. The pterygoids and palatines are much smaller than in *Amphisbaena* and the palate is less compact. As in *Amphisbaena*, there is no epipterygoid. There is no recognizable basitrabecular

process. There is no movement of the pterygoids as part of a maxillary segment, either of a mesokinetic or metakinetic type. In fact, *Glauconia* would appear to be akinetic and streptostylic.

Peters figures also the skull of *Typhlops* (*Onychocephalus*) *dinga*, which is mainly remarkable for the modifications of the jaws ; the anterior margin of the skull, the premaxillae, and the opposing lower jaw are without teeth, while the tooth-bearing maxillae are situated far back with the teeth directed backwards.

In this type and in *Glauconia* Peters identifies a large bone in the side wall of the skull, against which the quadrate articulates, as a temporale. It appears to me to have the position and relations of a prootic. In my *Glauconia nigricans* it certainly is a prootic. It is interesting in that its anterior ventral margin forms a projecting plate of bone which overlaps the lateral descending process of the parietal and forms a closed passage for the second and third branches of the trigeminal nerve, while the profundus branch passes forward inside the cranial cavity. The maxillary and mandibular branches pass to the exterior beneath the ventral margin of this ' prootic extension '. The skull of *Glauconia* described is that of a sectionized adult head, but it compares favourably with the ' prootic extension ' of *Acontias meleagris* shown in figs. 1 and 5. In the adult skull of the latter, as far as I can tell from a macerated specimen, the ' prootic extension ' does not overlap the parietal downgrowth, as in *Glauconia*, but forms a suture with it. There are no nerve foramina in this ' prootic extension ' of *Acontias meleagris*, but there is a gap ventrally between it and the margin of the basal plate, and presumably this is where one would find the exit of the maxillary and mandibular branches of the trigeminal. As already mentioned in the descriptive section, the profundus nerve in *Acontias* runs forward in a cavity between the dura mater and the membranous cranial wall, and this course is medial to the epipterygoid.

In my studies of *Glauconia nigricans* I found no projection from the margin of the basal plate to correspond to the projection in *Acontias* which I have marked with an ' *x* '. I was particularly looking for such a projection, because in a previous study of developmental stages of the snake *Leptodeira hotamboia* (1929), an Opisthoglypha, I had dignified such a projection in this snake as an ' epipterygoid ' (see fig. 10, Gaupp's bone).

The typical ophidian skull has a very unique appearance, but its peculiarities are all modifications to provide the wide gape of the specialized snake—that is, an extreme elongation and individual mobility of all the bones of the palate. When we discount these modifications we find that the remaining ophidian characteristics are those described for *Glauconia*, features which are all associated with a subterranean existence—the cranial box formed from the parietal and frontal downgrowths, the absence of temporal vacuities and arcades, the width of the orbitotemporal region, the smallness of the orbit ; the anterior tip of the skull in the specialized snakes, compared with the burrowing types, has lost its solidity and compactness.

In a previous section we have shown that these features are common to the burrowing lizards as well as to the burrowing snakes.

There are, however, certain characteristics which we regard as distinctively ophidian and as differentiating the snake from the lizard skull. Most discussed of any of these points has been the so-called ' alisphenoid ' of Parker

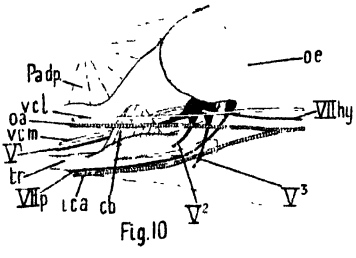


Fig.10

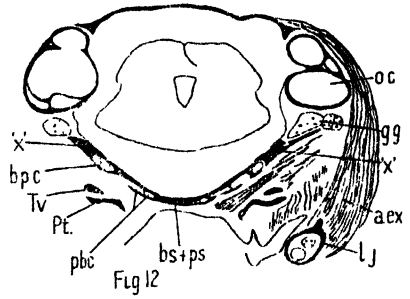


Fig 12

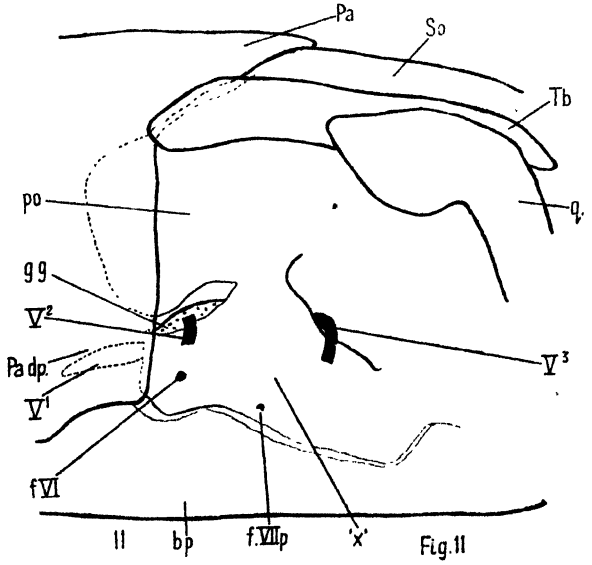


Fig.11

FIG. 10.—*Leptodeira hotamboia*, early embryo ; diagram from wax model, showing Gaupp's bone.

FIG. 11.—*Leptodeira hotamboia*, late embryo ; graphic reconstruction of otic and temporal regions, to show the bone ' *x* '.

FIG. 12.—Transverse section, *Leptodeira hotamboia*, late embryo ; demonstrating the relations of the bone ' *x* '.

(1878), ' prootic extension ' of Peyer (1912), ' laterosphenoid ' of de Beer (1926), and which I described as an ' epipterygoid ' (1929). This structure is recognizable in the adult snake skull as a bone of the side wall in the orbitotemporal region, closing the prootic incisure of the chondrocranium, and penetrated by

foramina for the maxillary and mandibular branches of the trigeminal. The profundus, with the optic and eye muscle nerves, all emerge through a foramen orbitale magnum. Peyer regarded the bone in question merely as an extension of the prootic bone, but it is not the 'prootic extension' of my *Glauconia* or *Acontias*. From his figures of his wax models it is the same structure as Parker's 'alisphenoid', and is as likely to be an extension of the basal plate as of the prootic. Furthermore, in *Tropidonotus* and *Pseudechis* (de Beer, 1926), and in *Leptodeira* (Brock, 1929), it arises in connection with the margin of the basal plate, and only at a late stage reaches to the prootic. De Beer considered that the structure could not be a processus ascendens (epipterygoid) because it had no relations with the pterygoquadrate; nor a pila antotica because it was behind the profundus; nor a pila lateralis, as in *Amia*, because it was median to the vena capitis lateralis. De Beer regarded it as part of the original cranial wall, possibly something peculiar to snakes, but to which he gave the name 'laterosphenoid'

In my study of *Leptodeira* I was impressed with the fact that this bony structure is supported upon a cartilaginous ledge of the basal plate. I suggested that this ledge was a basitrabecular process, otherwise absent in snakes, and regarded the bony structure as an epipterygoid resting upon the basitrabecular process, and incorporated in the cranial side wall, much as the alisphenoid of mammals (a visceral or splanchnocranial structure) is there incorporated in the side wall. It was not a very satisfactory suggestion: the so-called basitrabecular process has an unusually dorsal position for that structure. Moreover in the python there are very definite basitrabecular processes in front of this ledge of the basal plate.

The present study of *Acontias* makes it highly improbable that it was a correct interpretation. *Acontias* has a bony process, '*x*', of the basal plate similar in position and relations to the structure in snakes, and at the same time has an unmistakable and typical lacertilian epipterygoid and basitrabecular process.

In a late stage of an embryo of *Leptodeira* (figs. 11 & 12) one finds a probable explanation of the conflicting accounts of 'prootic extension' and 'alisphenoid' in the snake. In a graphic reconstruction (fig. 11) the bone '*x*' is shown wedged between the otic capsule and basal plate, and is overlapped anteriorly by the descending process of the parietal. The profundus nerve runs forward medial to '*x*' and to the descending process of the parietal. The maxillary branch of the trigeminal emerges from the cranial cavity between '*x*' and the otic capsule margin. Between this gap and the opening for V^3 the bone '*x*' is completely fused with the otic capsule wall, showing no line of suture, whereas there is a very definite line of suture between '*x*' and the basal plate. In transverse sections through this region (fig. 12) this line of suture is observable at the upper margin of the ossifying cartilage of the basal plate. The floor of the cranium, as usual, consists of two ossifications, the basiphenoid and the underlying membrane bone, the parasphenoid. Between them they enclose a parabasal canal. The bone '*x*' is supported on the lateral margin of the

basal plate, forming a suture laterally with the parasphenoid and medially with the basisphenoid. The more medial portion must be Gaupp's bone, described also by de Beer (1926) as 'laterosphenoid' and by me (1929) for young stages of snake embryos. But from this late stage of *Leptodeira hotamboia* it would seem that there may also be a ventral extension of the prootic, overlying and fusing with Gaupp's bone laterally. Whether this bone '*x*' is to be regarded as a bony extension of the basal plate which has fused with the prootic, or whether it is a composite bone from the fusion of a prootic extension with Gaupp's bone, nevertheless it deserves to be regarded as a discrete bone. Probably de Beer's term 'laterosphenoid' is the best name to apply to it, signifying that it is an ossification in the membrane of the true cranial side wall and not a splanchnocranial element.

I propose using the term 'laterosphenoid' for the bone '*x*' (Gaupp's bone) in *Acontias* as well as the snake.

It would be interesting to summarize the distinctive features of the snake skull which separate it definitely from the lizards. An epipterygoid is not only absent in snakes and in the burrowing amphisbaenid, but also independently in the chameleon. The basitrabecular process, though absent in most snakes, is present in the python, and it may be absent in lizards, e.g. *Amphisbaena*.

In Ophidia the platytrabic condition of the chondrocranium seems a distinctive feature, separating the group from Lacertilia, which seem to be invariably tropitrabic. The platytrabic condition of the snakes is obviously correlated with the formation of the broad cranial case in the orbitotemporal region and the disappearance of the interorbital septum. In this connection it would be interesting to know the condition of the trabeculae in *Amphisbaena*; conceivably this lizard might be platytrabic, but I have seen no account of its chondrocranial structure. De Beer (1937) has pointed out that the platytrabic condition is obviously the primitive one from which the tropitrabic has been independently derived in a number of types. Furthermore he has suggested that the occurrence of the platytrabic condition in Ophidia does not necessarily indicate their primitive nature, but merely that there has been an ontogenetic delay or hold-over of the paired condition of the trabeculae; the platytrabism persists instead of giving place to the tropitrabic condition. Gaupp (1903) and Versluys (1912) both considered the platytrabic condition a secondary modification from the tropitrabic reptilian condition.

In my description of the chondrocranium of *Leptodeira* (1929) I pointed out that the planum antorbitale was attached to the dorsal edge of the nasal septum by a commissure which was not a sphenethmoidal commissure. If the freedom of the nasal capsules ventrally is the primary condition in reptiles, as Gaupp thought, then this attachment in the snake is a secondary connection serving to support the olfactory capsules in lieu of sphenethmoidal commissures obliterated by the downgrowth of the frontal processes. The chameleon has such a secondary attachment of the planum antorbitale to the nasal septum, correlated with a telescoping of the back of the olfactory capsules.

Versluys (1912) described very carefully the mesokinetic condition of the ophidian skull. With the development of the wide cranial case formed by parietal downgrowths fusing with the otic capsules and the supraoccipital, there could be no longer the sliding contact between parietals and supraoccipital which characterizes the metakinetic reptilian skull. He pointed out that in the python, where basitrabecular processes are retained, there is a movable joint between pterygoids and basitrabecular process, and that the upper jaw and palate and nasal capsules were movable as one segment relative to the cranial case ; the sliding contact was between frontals and parietals, a mesokinetic condition. The akinetism of the Glauconidae is probably a secondarily degenerate condition.

Versluys emphasized particularly the fact that the amphisbaenid lizards were also mesokinetic, a fact which suggests that the transformation of a metakinetic type into a mesokinetic might have taken place more than once in a lacertilian stock which would be ancestral also to the Ophidia. The mesokinetism which I have described for *Acontias* shows that this transformation has taken place within a single group of lizards, the skinks.

In fact, in this comparative study of *Acontias* with other burrowing lizards and with snakes, I have detected no features in skull structure which differentiate the Ophidia from the Lacertilia. The burrowing lizards and burrowing snakes form an intermediate series which completely bridge the gap between the typical lizards and the specialized snakes. The same applies to limb structure. There are lizards with complete absence of limbs and there are snakes with vestiges of limbs and limb girdles.

What are the absolute characters which separate the Ophidia from the Lacertilia ? One is led to the conclusion that the old view of the lacertilian origin of the snakes is the sound view.

Lettering of figures.

A., angular.
a.co., aditus conchae.
a.ex., adductor externus muscle.
b.p., basal plate.
bp.c., ,, ,, cartilage.
bs.ps., basisphenoid plus parasphenoid.
bt.p., basitrabecular process.
c.a., columella auris.
ec.c., ectochoanal cartilage.
ept., epipterygoid.
f.ep., foramen epiphaniale.
f.g., facial ganglion.
f.n., fenestra narina.
Fr., frontal.
f.su., fenestra superioris.
G.b., Gaupp's bone.
g.g., Gasserian ganglion.
hyd., hyoid.
hy.f., hypophysial fenestra.
i.c.a., internal carotid artery.
i.s., interorbital septum.
Ju., jugal.
l.j., lower jaw.
M.c., Meckel's cartilage.
Mx., maxilla.
Na., nasal.
n.p., nasal process.
n.s., nasal septum.
o.a., orbital artery.
o.c., otic capsule.
olf., olfactory capsule.
Pa., parietal.
pa.c., paraseptal cartilage.
Pal., palatine.
p.ant., planum antorbitale.
pb.c., parabasal canal.

Lettering of figures (cont.).

p.ex., prootic extension.
Pmx., premaxilla.
po., prootic.
Pof. postfrontal.
Prf., Prefrontal.
pr.pt., protractor pterygoideus muscle (constrictor dorsalis).
psd., pseudotemporalis muscle (adductor internus).
Pt., pterygoid.
ptd., pterygoideus muscle (adductor internus).
Pv., prevomer.
q., quadrate.
so., supraoccipital.
sph.c., sphenethmoidal cartilage.
Sq., squamosal.
ss., supraseptal cartilage.
Tb., tabular.
t.c., trabeculum communis.
t.m., taenia marginalis.
tr., trabeculum.
ts.pa., tectum synoticum, processus ascendens.
Tv., transversum.
v.c.l., vena capitis lateralis.
v.c.m., vena capitis medialis.
'*x*', 'laterosphenoid'.
z.a., zona annularis.
*, frontal-parietal sliding contact.
II, optic nerve.
V^1, profundus branch of trigeminal nerve.
V^2, maxillary branch of trigeminal nerve.
V^3, mandibular branch of trigeminal nerve.
VI, abducens nerve.
*f.*VI, foramen abducens.
VII *cht.*, chorda tympani branch of the facial nerve.
VII *hy.*, hyomandibular branch of the facial nerve.
VII *p.*, palatine.
*f.*VII*p*, foramen for palatine nerve.

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On the Larvae of certain Crustacea Macrura, mainly from Bermuda.

By ROBERT GURNEY, D.Sc., and MARIE V. LEBOUR, D.Sc., (Naturalist at the Plymouth Laboratory).

(With 26 Text-figures *)

[Read 9 May 1940]

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INTRODUCTION.

The following series of papers is mainly the result of work done at the Bermuda Biological station, though some use has also been made of material from the *Discovery* Expedition. One of us (R. G.) spent some weeks at Bermuda in the spring of 1935 and summer of 1938, while the other (M. V. L.) worked there for a whole year from July, 1938.

For the wonderful facilities offered by this excellent station for the study of oceanic Decapoda we are most grateful to the Director, Dr. J. F. G. Wheeler, to his staff and to Captain Whitfield and the crew of the *Culver*, who spared no effort to help in obtaining material. We gratefully acknowledge also the assistance rendered by the crew of the Woods Hole Research ship *Atlantis*, by kind permission of Dr. Iselin, during her visit to Bermuda in 1938. We owe more than we can express to the encouragement and help of Dr. Kemp, who has always been ready to place his unrivalled knowledge of the Decapoda at our disposal.

In each of the papers the list of literature given is confined to those papers which are not included in Gurney, 'Bibliography of the larvae of Decapod Crustacea' (Ray Society, 1939).

* The cost of the reproduction of these illustrations has been borne by the Westwood Fund.

1. Larvae and Post-larvae of *Acanthephyra purpurea*, *Discias atlanticus* and some related forms. By MARIE V. LEBOUR.

The larval and post-larval history of *Acanthephyra purpurea*, which is common in the Bermuda plankton, has been followed from the first to the last larva, the latter changing to the post-larva. This is distinct from the *A. purpurea* whose larvae are described by Kemp (1907) which is now known to be *A. haeckeli* (von Martens); see Kemp (1939) (=*A. purpurea* var. *multispina* Coutière). Another common form is the larva of *Discias atlanticus*, the adult of which has been described by Gurney (1939). The position of *Discias* is a matter of controversy, but the larval stages are in many ways very like those of *Acanthephyra*, and there can be little doubt that they are related. Moreover, two other larvae which were found fit into a series beginning with *Acanthephyra*, through an unknown species which is almost certainly allied, and another unknown form which has the legs modified like *Discias*, to *Discias* itself. These peculiarly modified legs seem to indicate a life of commensalism, probably with a sponge, for Kemp's (1920) species, *Discias exul* from the Andamans, was found on a yellow sponge. Thus we now know the larval stages of *Acanthephyra* and of *Discias* with the post-larvae. The other two are not attributable to any adult, but from their structure appear to have affinities with both *Acanthephyra* and *Discias*.

ACANTHEPHYRA PURPUREA A. Milne-Edwards. (Fig. 1, *a–x*; Fig. 2, *a–s*.)

This larva occurs commonly in the outside Bermuda plankton, from about 100 to 300 metres, occasionally in shallower or deeper water. The first and the last larvae were obtained, and most of the intermediate stages. Adults and young stages were obtained in June 1939, at 750 to 800 metres, a few miles from Bermuda. The larvae occurred throughout the year.

Colour.—The larvae are very transparent, with red chromatophores scattered sparsely on the body, and congregated especially in the hump. The third abdominal somite is full of fatty material, and projects out as a hump, and the body is bent at this point at almost a right angle. It is the same with the other three larvae described below, which all have a pronounced hump full of fatty material, and the body much bent.

First larval stage. (Fig. 1, *a–c*.) Length 3·4 mm. (fig. 1, *a*) including rostrum. The rostrum projects beyond the sessile eyes. The carapace is denticulate antero-ventrally. The antennal scale is jointed at the tip, and there are two outer marginal setae. The flagellum is a long slender rod with an accessory seta at about half its length. There are rudiments of the first legs and minute lateral spines on the fifth abdominal somite (fig. 1, *b*). The exopods of the maxillipedes bear four setae. The telson (fig. 1, *c*) is much indented in the centre and bears 7+7 setae.

Second larval stage. (Fig. 1, *d–g*.) Length ca. 4 mm. Very like the first, but with the eyes free on long stalks (fig. 1, *d*, *e*). The rostrum is not quite as long as the eyes. There are rudiments of two legs. The telson has 8+8

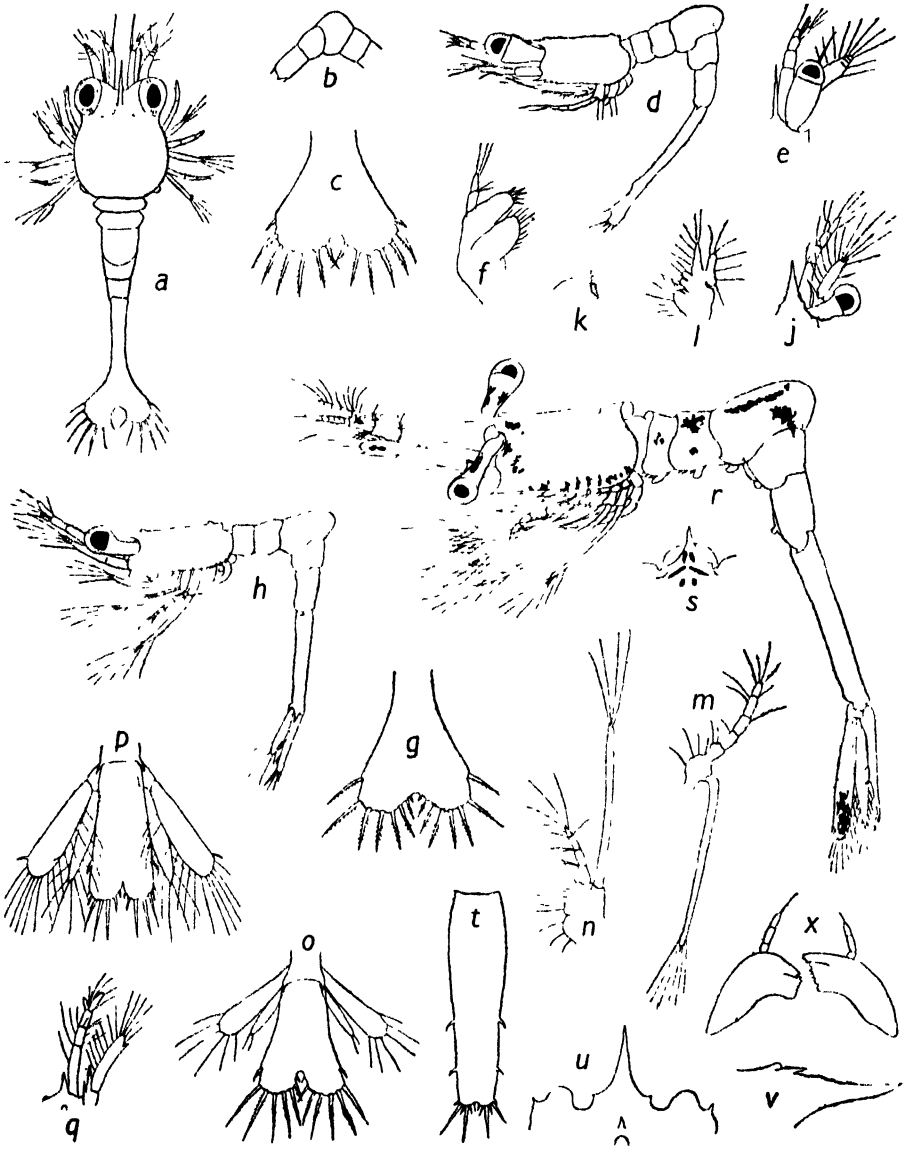

FIG. 1.—*Acanthephyra purpurea*. *a*, first larva, 3·4 mm. long; *b*, side view of abdomen; *c*, telson; *d*, second larva, 4 mm. long; *e*, rostrum etc.; *f*, maxillule; *g*, telson; *h*, third larva, 4·5 mm. long; *j*, rostrum etc.; *k*, mandible; *l*, maxilla; *m*, third maxillipede; *n*, first maxillipede; *o*, telson; *p*, fourth larva, telson; *q*, rostrum etc.; *r*, seventh larva, 7 mm. long; *s*, rostrum; *t*, telson; *u*, last larva, rostrum and anterior part of carapace, dorsal; *v*, rostrum; *x*, mandible.

setae (fig. 1, *g*). There are denticulations both anteriorly and posteriorly on the carapace. The antennal scale is still jointed, but the accessory seta has disappeared from the flagellum. The mandible has rudiments of cutting and molar parts; the maxillule (fig. 1, *f*) has an outer prominence indicating the exopod, but without setae, a two-segmented endopod with three terminal setae and two lateral setae, and the inner lobes are well developed. The maxilla has four well-developed inner lobes and an unsegmented setose endopod.

Third larval stage. (Fig. 1, *h*, *o*).—The rostrum is shorter and triangular. There are small supra-orbital spines. The denticulations on the carapace have disappeared in front, but are still present posteriorly. The antennal scale is still slightly segmented, but the flagellum is much reduced. The mouth-parts are much as in stage II (fig. 1, *k*, *l*). The maxillipedes have 4, 6, 6 setae. The telson is an elongated triangle, indented in the centre with 8+8 setae (fig. 1, *o*). The inner uropods have two setae. Legs 1 and 2 are slightly longer, and leg 3 has appeared.

Fourth larval stage. (Fig. 1, *p*, *q*.) Length 5 mm. The rostrum is very short. The antennal scale is not segmented, and there are no lateral setae. The flagellum is very short. There are rudiments of all the legs and legs 1 and 2 are functional. The spine on abdominal somite 5 is curved. The telson is much elongated (fig. 1, *p*), still indented at the hind margin. The denticulations on the carapace are still present behind, but there are none in front and none as yet on the abdominal somites. The proximal segment of the antennular peduncle bears a spine ventrally.

Fifth larval stage, length ca. 5·2 mm. Leg 4 is bilobed, but still rudimentary. There are no pleopods. The telson is greatly elongated.

Sixth larval stage, length ca. 6 mm. All the legs but the fifth are functional. There are very small pleopods.

Seventh larval stage. (Fig. 1, *r–t*). Length 7 mm. The rostrum is still very short and the supra-orbital spines very small (fig. 1, *s*). The spine on the ventral surface of the proximal antennular segment is very large, but quite smooth. The carapace ends anteriorly in a sharp spine, but there are no denticulations anteriorly, although they still persist posteriorly. There are a few denticulations on the pleura of abdominal somites 1 and 2. All the legs are present with setose exopods, but the last endopod is still bent under the body. The exopods of legs 1–4 have eight setae. The lateral spines on the fifth abdominal somite are large and recurved. The pleopods are short. The telson (fig. 1, *t*) is long and narrow, with two pairs of lateral spines behind the first half, and twelve terminal spines, the hind margin being still indented.

After this there appear to be several stages up to the last, which is 12 mm. long. The legs are all functional, the pleopods lengthening. The mandibular palp does not appear until a length of ca. 9 mm., in which stage the pleopods are long and slender. The palp is uniramous with one terminal seta. The penultimate stage seems to vary between 9 and 10·5 mm. At 10·5 mm. the palp may have two segments, and the rostrum may have from one to four dorsal

teeth. (On the other hand, the last stage may have the rostrum with only one tooth.) The telson may have twelve or ten terminal spines, and in the older stages is rounded at the tip. The pleopods are not setose.

Last larval stage. (Fig. 1, *u–x*; Fig. 2, *a–k*.) Length ca. 12 mm. This stage is very like the penultimate one, but the mandibular palp is 3-segmented (fig. 1, *x*). There are denticulations posteriorly on the sides of the carapace and on the pleura of somites 1 and 2. The rostrum is short and may have one to four dorsal teeth (fig. 1, *v*). The antennular peduncle still bears a large smooth spine ventrally (fig. 2, *j*) The maxillule (fig. 2, *a*) and maxilla (fig. 2, *b*) have hardly altered from the early stages. The first and second legs end in simple dactyls. Legs 1–4 bear epipods. The pleopods are slightly setose terminally (fig. 1, *f*, *g*). The telson bears ten or eight terminal spines, and may have two or three pairs of lateral spines. The last larval stage changed to a post-larva on March 4 1939.

Post-larval stage from last larva (Fig. 2, *l–s*.) Length ca. 12 mm. (fig. 2, *l*). This is the 'parva' stage of Coutière (1906 *a*). The rostrum is still very short, not reaching to the eyes, and bears five dorsal teeth and one ventral tooth. The eye is small, but the stalks are fairly long. There are no denticulations on the carapace, but they persist on the first and second abdominal somites (fig. 2, *n*). There is an antennal and pterygostomial spine, but no supra-orbital. The large spine on the antennular peduncle has disappeared. There are epipods on the maxillipedes and legs 1–4, and long exopods bearing many setae on maxillipede 3 and legs 1–5. The first and second legs are chelate, the first (fig. 2, *o*) stronger than the second (fig. 2, *p*). The second leg has a short thick spine on the merus, the third three (fig. 2, *q*) spines on the ischium, two on the merus, the fifth (fig. 2, *z*) two on the ischium, and two on the merus. These spines are long on the fifth leg. The telson (fig. 2, *s*) has four pairs of lateral spines, and terminates in a central tooth and six spines.

In comparing the larvae of *A. purpurea* with Kemp's description of *A. haeckeli*, we find that they resemble one another closely in general features. The following differences may, however, be pointed out: There is no large spine described or figured on the antennular peduncle in *A. haeckeli*, though this is conspicuous in all but the early stages in *A. purpurea*, and the maxillular palp is not distinctly divided, nor is there a prominence representing the exopod as in *A. purpurea*. There are no denticulations on the abdominal somites in *A. haeckeli*, although the posterior denticulations occur on the carapace as in *A. purpurea*. It seems almost certain that the earliest stage described in *A. haeckeli* is the second larval stage, as the telson bears 8+8 spines and the eyes are free. Gurney's larva (1924 *c*, fig. 41, p. 111) of an *Acanthephyra* (?) larva almost certainly belongs to *A. purpurea*. Coutière's *Hoplocaricyphus similis* has been ascribed by Murray and Hjort (1912) to *A. multispina*, but almost certainly belongs to *A. purpurea*. Coutière (1906 *a*) describes the metamorphosis in *A. purpurea* from post-larva through the young stages to the adult showing the transformation of the rostrum from very short to very long.

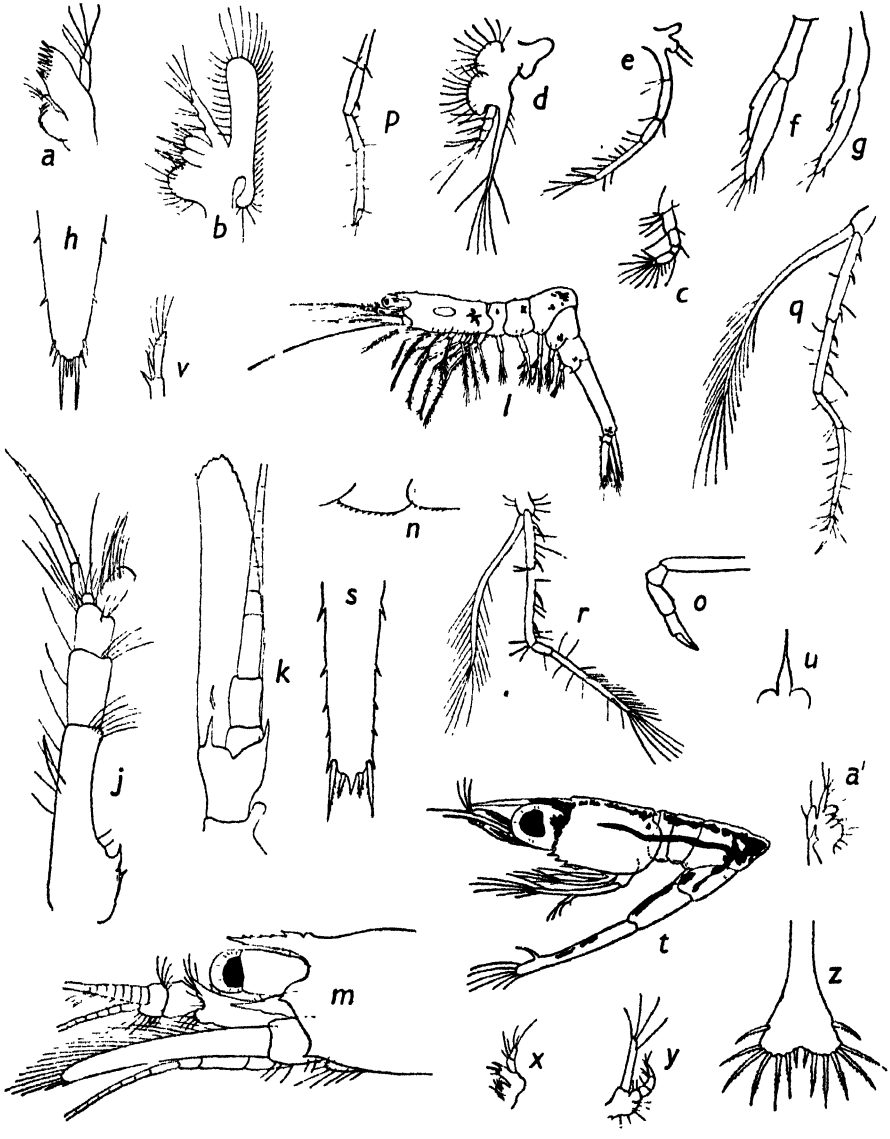

FIG. 2.—*a–s. Acanthephyra purpurea.* *a*, last larva, maxillule; *b*, maxilla; *c*, second maxillipede; *d*, first maxillipede; *e*, third maxillipede; *f*, fourth pleopod; *g*, fifth pleopod; *h*, telson; *j*, antennule; *k*, antenna; *l*, post-larva, ca. 12 mm. long; *m*, anterior end; *n*, pleura of first and second abdominal somites; *o*, first leg; *p*, second leg; *q*, third leg; *r*, fifth leg; *s*, telson; *t–z*, *a'*, *Discias atlanticus*; *t*, first larva, 2·5 mm. long; *u*, rostrum; *v*, antenna; *x*, maxillule; *y*, second maxillipede; *z*, telson; *a'*, maxilla.

Thus the larva, as is shown by Kemp for *A. haeckeli*, and in the present work for *A. purpurea*, begins with a long unarmed rostrum which is generally reduced. This lengthens again in the late larval stages through the post-larva ('parva' form) in which it is still short, to the very long rostrum of the adult. The eye is much reduced at the post-larval stage.

DISCIAS ATLANTICUS Gurney. (Fig. 2, *t–z*, *a'*; Fig. 3, *a–z*.)

The adult of this species has been described by Gurney (1939) from Bermuda. It was obtained in plankton from shallow water in the Reach in July 1938. The larvae in several stages were in the tow-nets from outside, from depths ranging from about 60 to 300 metres. A post-larva was obtained from a last larva in the laboratory. Its characters are almost exactly those of the adult, the appendix masculina being already present, and the length the same as Gurney's specimen. The larvae are highly coloured with orange and red chromatophores, red on the rostrum, antennular peduncle, and eye-stalk, all along the thorax laterally and (or) dorsally, and along the abdomen, especially on the hump. The body is usually bent at an acute angle. The rostrum is long and smooth in all stages. There is no mandibular palp in the larvae except a very minute rudiment in the last stage.

First larval stage. (Fig. 2, *t–z*, *a'*.) Length 2·5 mm. including rostrum. The whole body is yellow, with a good deal of red (fig. 2, *t*). The eyes are sessile and the rostrum long. There are three denticles ventrally on the anterior end of the carapace. The antennular peduncle is unjointed, the inner flagellum being a long simple seta, the outer with three aesthetes. The antennal scale is jointed at the tip with two outer setae, the flagellum being a short rod with two setae at the tip (fig. 2, *v*). There is a stout inner spine at the base. The rostrum is simple (fig. 2, *u*), swollen at the base and ending in a sharp point. The maxillule has a prominence representing the exopod, but not setose, a 2-segmented endopod with three terminal and three lateral setae, and two well-developed inner lobes (fig. 2, *x*). The maxilla (fig. 2, *a*) has the proximal lobe well developed, an unsegmented endopod with six setae and an exopod with three setae. The first maxillipede has an exopod with five setae, an unjointed setose endopod and inner setose lobe. The second maxillipede (fig. 2, *y*) has an exopod with four setae and an endopod of four segments, the third maxillipede (fig. 3, *a*) has a long exopod with five setae and a 4-segmented endopod. There are no rudiments of legs. The telson (fig. 2, *z*) is slightly indented at the hind margin with 7+7 setae. There are no lateral spines on the abdominal somites.

The second stage was not obtained.

The third larval stage. (Fig. 3, *b*, *c*.) Length 3·2 mm. The first leg is present, but not functional. The antennal scale is no longer segmented. There are denticulations anteriorly on the carapace but not posteriorly, but none on the abdominal somites. There are no lateral spines on the fifth abdominal somite and no spines on the antennular peduncle. The telson (fig. 3, *c*) is

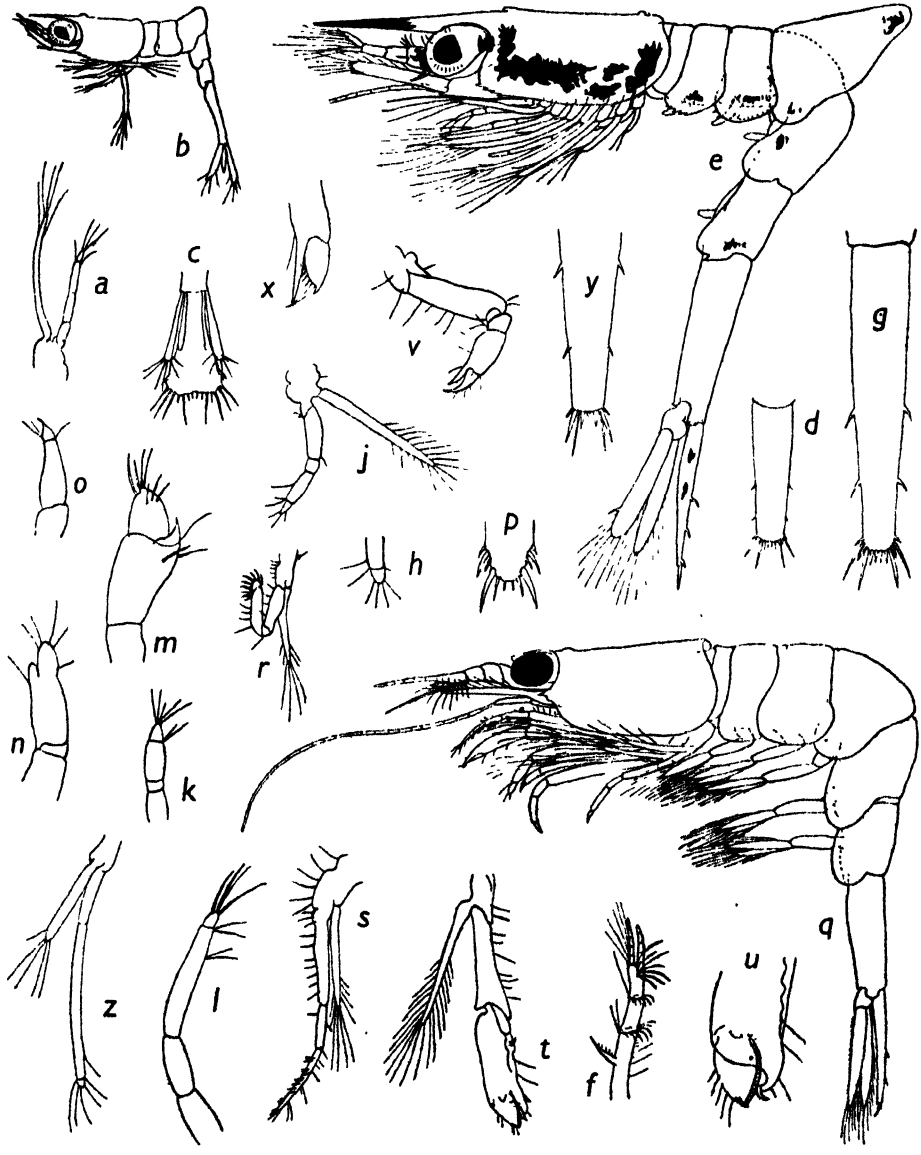

FIG. 3.—*a–y. Discias atlanticus.* *a*, second larva, third maxillipede; *b*, third larva, 3·2 mm. long; *c*, telson; *d*, telson of fifth larva; *e*, penultimate larva, 10 mm. long; *f*, antennule; *g*, telson; *h*, tip of first leg; *j*, second leg; *k–p*, cast skin of last larva; *k*, tip of second maxillipede; *l*, third maxillipede; *m*, first leg; *n*, second leg; *o*, third leg; *p*, telson; *q*, post-larva, 11 mm. long; *r*, second maxillipede; *s*, third maxillipede; *t*, first leg; *u*, first leg, chela; *v*, second leg; *x*, second leg, chela; *y*, telson; *z*, Species C, last larva, third maxillipede.

elongated, and the hind margin only very slightly indented. The inner uropods are not setose.

The fourth larval stage was not obtained.

The fifth larval stage. (Fig. 3, *d*.) Length 5·5 mm. The first and second legs have setose exopods, 3–5 rudimentary. The telson is long and narrow, rounded posteriorly, with twelve setae and two pairs of lateral spines behind the first half. There are denticulations on the carapace anteriorly and posteriorly, and on the first abdominal somite. The fifth abdominal somite has lateral spines. There is a large spine ventrally on the proximal segment of the antennular peduncle.

The sixth stage was not obtained, and the next is probably stage VII.

The seventh larval stage, length 8 mm. There are denticulations on the carapace both anteriorly and posteriorly and on abdominal somites 1 and 2, only very few on 2. All the legs have exopods, although the last two are very small, and the endopods rudimentary. The pleopods are small.

The eighth larval stage (penultimate). (Fig. 3, *e–j*.) Length 10 mm. Very like stage VII, but with longer pleopods. There is no trace of a mandibular palp. The telson (fig. 3, *g*) is slightly rounded posteriorly, and bears twelve spines terminally and two pairs of lateral setae behind the first half. The chelae are not yet formed, and the endopods of legs 4 and 5 are still very short. There is a very large serrated spine ventrally on the proximal antennular segment (fig. 3, *f*).

The ninth larval stage (last). (Fig. 3, *k–p*.) Length 12 mm. Very like the penultimate stage. The mouth-parts have hardly changed from the first stage, but there is a minute trace of a mandibular palp, and the cutting and molar portions are distinctly divided. Legs 1 and 2 are chelate and modified, the second with the chela (fig. 3, *n*) incomplete. The endopods of legs 4 and 5 are jointed, but short. The pleopods are not very long, but have a few setae at the tips. The carapace is still slightly denticulate anteriorly and posteriorly, and on the first and second abdominal somites. The tip of the telson (fig. 2, *p*), is pulled out, and is armed with twelve spines and two pairs of lateral spines. There are no epipods on the legs.

This stage changed to the post-larva.

Post-larval stage, from last larva. (Fig. 3, *q–y*.) Length 11 mm. This stage is very like the adult, and the same size as Gurney's male specimen, and already shows an appendix interna on the second pleopods. The specimen was not dissected, but the second and third maxillipedes and legs, and also the whole of the form of the body, agree with the description of the adult very closely. The telson (fig. 3, *y*), however, is not so pointed, and has four spines on each side of the central tooth. Gurney (1939 *b*) has shown that *Leptochela bermudensis* reaches full development and sexual maturity at a remarkably early stage, and it would seem that *Discias* does the same.

Species D. (Fig. 4, *a–f.*)

This species, only found in the late larval stages (probably VIII and IX), occurred sparingly in the outside plankton of Bermuda from about 250 to 450 metres. In the peculiar modification of its legs it has a very close resemblance to *Discias*. Its general appearance, however, is more like species C, which has the legs unmodified, and both C and D have epipods on legs 1–4. All the specimens obtained alive had a number of fatty globules in the thorax. The larvae are very transparent, with pale red on the thorax, antennules, eye-stalk, and rostrum. On the abdominal somites 1 and 2 there were lines picked out with yellow.

The eighth larval stage. Length 7 mm. The rostrum is short. It is broad at the base, with lateral denticulations, and ends in a smooth point. The carapace has denticulations antero-ventrally and postero-ventrally, and the first and second abdominal somites are denticulated, with many denticulations on somite 2. There are thin bilobed pleopods. There is a strongly recurved lateral spine on abdominal somite 5, and a long straight spine on 6. The first and second legs are beginning to widen, legs 4 and 5 are well developed, and there are exopods on all the legs. The telson is slightly rounded at the hind end, with twelve spines and two pairs of lateral spines. There is a large spine ventrally on the proximal segment of the antennular peduncle.

The ninth larval stage, probably the last. (Fig. 4, *a–f.*) Length 8·5 mm. Very like stage VII. There are small epipods on legs 1–4, the pleopods are slightly setose, and the legs further developed. Leg 1 (fig. 4, *d*) has a rounded dactyl, as in *Discias*, and the second (fig. 4, *e*) is modified as in that genus. The mouth-parts are very like those of *Discias*, but there is no mandibular palp in this larva. The maxillule has a two-segmented endopod and well-developed endites, and there is a slight prominence in the position of the exopod. The maxilla has a well-developed proximal lobe and an unsegmented endopod with setae. The telson is nearly straight and bears twelve terminal spines, and two pairs of lateral setae behind the first half.

A later stage occurred measuring 11 mm. in length, which had larger and more setose pleopods. Otherwise it is much like the last, and it is probable that it was an alternative last stage having stayed longer in its larval form prior to metamorphosis.

Species C. (Fig. 3, *g*; Fig. 4, *g–v.*)

This species, which is probably the *Caricyphus serramarginis* of Bate (1888), changed from the last larval stage to the post-larval in the laboratory. Only late larvae were seen in the plankton, and these very rarely. They occurred outside from about 250 to 300 metres. The larva closely resembles D in general form, but legs 1 and 2 are not modified, and there is a dorsal tooth at the posterior end of abdominal somite 3. It has the same pale red colouring

as D, but it is more diffuse and extends on to the abdomen, especially on segments 1–3 and into the hump, which is rather larger than it is in D. It is so like D in many ways that there seems almost certainly some relationship, but the larva and post-larva in many respects resemble *Acanthephyra*. It is probable that this also has affinities with the Hoplophoridae, and possibly links *Acanthephyra* to *Discias*.

Stage VII (?), length ca. 6 mm. This is very like the last stage, only with short pleopods and the legs not quite so long.

Stage IX (?), last larval stage. (Fig. 4, *g–o*.) Length 8·6 mm. The rostrum is broad at the base with denticulate edges, and at about half its length there is a lateral tooth, the distal half is narrow, smooth, and pointed. There is a large spine ventrally on the proximal segment of the antennular peduncle. The mouth-parts resemble those of *Discias*, but there is no mandibular palp at this stage. The carapace is denticulated antero-ventrally and postero-ventrally, and there are denticulations on the first and second abdominal somites. The legs (fig. 4, *m–o*) end in long dactyls, and the exopods present on all the legs have many setae. There is a recurved lateral spine on abdominal somite 5, and a straight one on the sixth. The telson is slightly rounded behind, with twelve spines, and there are two pairs of lateral spines behind the first half. The pleopods are slightly setose. In all external features except the legs this larva resembles D, and is obviously related. It also possesses very small epipods.

Post-larval stage from last larva. (Fig. 4, *p–v*.) Length 8·64 mm. The rostrum (fig. 4, *q*) is straight, reaching beyond the eye, and armed with five dorsal teeth and one ventral near the tip. An antennal spine is present. There is a recurved lateral spine on the fifth abdominal somite. There are well-developed exopods on all the legs. The second maxillipede has the dactyl normally placed (fig. 4, *r*). The first leg (fig. 4, *t*) has a very short carpus, long propodus and fairly small and narrow chela, the second leg (fig. 4, *u*) with narrower chela. The third to the fifth legs ending in a long pointed dactyl, the third with four teeth on the merus, the fourth with two on the ischium and four on the merus, the fifth with one on the ischium and four on the merus. The telson (fig. 4, *v*) with a pointed central tooth and six spines, the outer one tooth-like, and an inner pair of hairs. There are two pairs of lateral teeth behind the first half, and the lower two-thirds of the margin is armed with short hairs laterally. The outer uropod has short setae all along the outer margin and hairs internal to them, and a sharp tooth near the end. A short curved division nearly cuts off the end, but not completely. Epipods were not seen, and unfortunately this specimen was lost before further details were made out, but many of the characters resemble *Acanthephyra*, whilst the larva has undoubtedly resemblances to Species D.

Having now found the larva of *Discias* it is a question, almost certainly answered in the affirmative, whether it is related to the Hoplophoridae. Gurney (1939), in reviewing the various suggestions as to its relationships, discusses

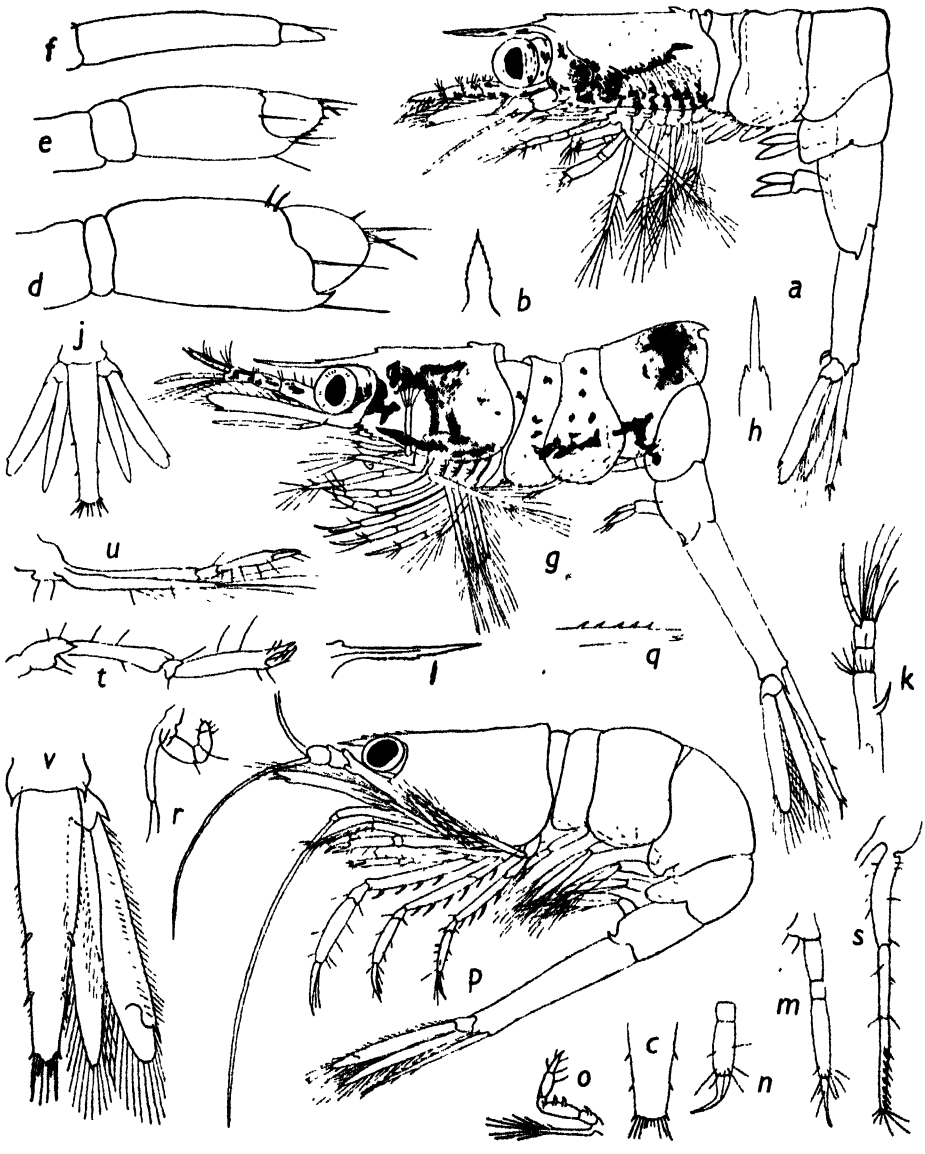

FIG. 4.—*a–f*. Species D. *a*, last larva, ca. 8·5 mm. long; *b*, rostrum; *c*, telson; *d*, first leg; *e*, second leg; *f*, third leg; *g–v*. Species C. *g*, last larva, ca. 8·6 mm. long; *h*, rostrum; *j*, telson; *k*, cast skin, last larva, antennule; *l*, rostrum; *m*, first leg; *n*, third leg; *o*, last leg; *p*, post-larva, ca. 8·6 mm. long; *q*, rostrum; *r*, second maxillipede; *s*, third maxillipede; *t*, first leg; *u*, second leg; *v*, telson.

the position, and is of the opinion that it seems to have some real affinity with *Bresilia* (Calman 1936), retaining some primitive features of the Pasiphaeidae and the Hoplophoridae. Chace (1939, 1940) has recently published a preliminary note and description on the new genus *Lucaya*, which he places in the Bresiliidae, and this, unlike *Bresilia*, has exopods on all the legs and normal pleurobranchs. This is very like species C described above, and brings all these forms close together. There are distinct resemblances between the larva of *Discias* and that of *Acanthephyra*, although there are very important differences. The two other larvae C and D, obtained only in the late stages, and in the case of C reared to the post-larva, seem to form a series with *Discias* and *Acanthephyra*. Thus we have the gradual series *Acanthephyra*—C–D—*Discias* and the last three all seem to be related to the Hoplophoridae. D has the legs modified as in *Discias*, but possesses small epipods on the legs, and in almost every other way resembles C, which has unmodified legs and is the nearest to *Acanthephyra*. The characters which these four larvae have in common are the following :—

(1) there are exopods on all the legs ;

(2) the maxillule has a 2-segmented setose endopod and well-developed endites (in the two species where the early larva is known (*Acanthephyra purpurea* and *Discias atlanticus*), there is a non setose prominence representing the exopod ;

(3) the maxilla has the proximal lobe well developed and a non-segmented setose endopod ;

(4) the carapace is denticulated posteriorly and (except in *Acanthephyra*) anteriorly, and there are denticulations on the first and second abdominal somite in the later larvae ;

(5) there is a marked hump on the third abdominal somite, a recurved spine on the fifth and a straight spine on the sixth, except in the very early larvae ;

(6) there is a very large spine ventrally on the proximal segment of the antennular peduncle in all but the very early stages ;

(7) the body is permanently bent at almost a right angle, or an acute angle ;

(8) the telson in the late larval stages has twelve terminal spines (reduced to eight in the late larva of *Acanthephyra*), and two pairs of lateral spines behind the first half.

In *Acanthephyra purpurea* and *Discias atlanticus*, the two extremes of the series, the larva is hatched with a rostrum and the telson is indented posteriorly.

Of these characters there stand out as very distinct the presence of exopods on all the legs, the very large ventral spine on the proximal segment of the antennule, and the denticulations on the posterior end of the carapace and on the first and second abdominal somites.

It is interesting to find that in the larva and post-larva of *Leptochela pugnax* described by Gurney (1936 *a*) the posterior margin of the carapace is also denticulated, and in the post-larva the abdominal somites also.

Whether Species D should be included in the genus *Discias* is doubtful. If we regard it as a *Discias*, then the genus would have to be modified to include it. *Discias exul* Kemp (1920) differs in several ways from *D. atlanticus*, being in some respects more primitive and in others less so. Knowing only the larva it is difficult to say much about the present species, but it possesses small epipods, which character alone shows it to be more primitive than any known species of *Discias*. Gurney (1936 *a*, 1939) has shown that Ortmann's larval genus *Anisocaris* almost certainly belongs to *Discias*, and has the legs modified as in that species. The two species known, *A. puerilis* described by Coutière (1907 *a*) and *A. dromedarius* by Ortmann (1893), resemble very closely the larva of *Discias atlanticus*. Coutière's species is not old enough to show the modified legs, but its form is so like that of *D. atlanticus* that it must belong to that genus. It seems likely that as the external form of D differs in several points from the known larva of *Discias* and of *Anisocaris*, and it alone possesses epipods, it should belong to another genus, but closely related. Species C resembles D in external features much more than it resembles *Discias*, but it has the legs unmodified as in *Acanthephyra*. In certain other ways it comes close to *Acanthephyra*, and seems to connect *Acanthephyra* with the *Discias*-like forms.

It is probable that the species of *Discias*, D, and the other *Anisocaris* larvae belong to one group, and that these are specially modified for the same way of living, probably with sponges, D being the most primitive of these. C, possibly identical with or related to *Lucaya*, connects the *Discias* group with *Acanthephyra*, having affinities with both. *Acanthephyra* belongs to the Hoplophoridae, and the other three are almost certainly closely related but belong to separate families, having no near affinity with the Pasiphaeidae, and it would seem also that the Bresiliidae come very close to the Hoplophoridae.

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2. The larvae of *Hoplophorus* and *Systellaspis*.

By Robert Gurney.

The genera of the Hoplophoridae fall into two groups, according to the size of the eggs :—Large eggs : *Hoplophorus*, *Systellaspis*, **Ephyrina*, *Hymenodora* ; small eggs : *Acanthephyra*, *Notostomus*.

The development of *Acanthephyra* is fully described by Miss Lebour, and includes a long series of normal larval stages. Presumably the same will be found to be the case in *Notostomus*.

In *Hymenodora* (Stephenson, 1935, p. 68) the large egg gives rise to a larva with rudiments of all appendages, but five stages are passed through before the post-larval form is assumed.

The following description of the larvae of *Systellaspis* and *Hoplophorus* will show how closely alike these genera with large eggs are in their development.

I. Systellaspis. (Figs. 5–6.)

The development of *Systellaspis* has been described in part by Coutière (1906 *a*), and more fully by Kemp (1910). Kemp has shown that there is at least one earlier stage than the first figured by Coutière, and has described a stage transitional between the larval and post-larval forms.

I have had the opportunity of examining a number of specimens taken from deep water off Bermuda, and some from the *Discovery* collections, and this material permits of giving a fuller account than has been possible hitherto.

The specimens from Bermuda belong to one species, and that species is probably *S. debilis*, since several half-grown specimens and one adult female with eggs were taken at the same place and the same time as the larvae. As will be pointed out, there is some difference in form of telson between the Bermudan larvae and those figured by Coutière and Kemp, and I also have a specimen from the *Discovery* material which has the same form of telson. It is uncertain if this form represents a distinct species, or possibly a stage in the development of *S. debilis* which is not represented in the Bermudan material.

The egg and embryonic telson.

The egg of *S. debilis* is very large, measuring according to Kemp 3·2 × 2 mm., and 3·5 × 2 mm. according to Coutière. In my Bermudan specimen they may be as long as 4·0 mm. (fig. 5, *a*.)

The structure of the telson is of some interest. In all Caridea which have been examined the embryonic telson has six transparent outgrowths enclosing the seven setae of the larva, the sixth and seventh being enclosed in one envelope. In larvae of *S. debilis* which are not near hatching six setae can be seen, each enclosed in its own envelope, the seventh, innermost, seta not having appeared as yet. At later stages the outer envelopes are pressed together and it becomes impossible to determine their limits, but there is certainly a seventh seta.

* I am indebted to Dr. S. W. Kemp for information as to the size of egg in *Ephyrina*.

Miss Lebour has kindly allowed me to use a figure of her own taken from a larva very near hatching. In this specimen the seven setae of the larval telson are setose, and each is enclosed in a non-setose envelope, fitting close to it, and distinct from the large outer envelopes. Nothing of this kind has been seen in any other Carid, and it seems that the explanation must be that there is an additional moult in the egg, the first free larva then being actually the second stage of the normal sequence.

The Larvae

The larvae, when brought up alive, swim feebly, back down and tail first; but, when dead, they float back upwards. One lived for a day in a refrigerator, but did not moult. They were only taken in deep water with 1500 metres of wire out.

The whole body is orange-red except the thorax, which is filled with dark red yolk.

Stage 1. Fig. 5, *d–g* (see Kemp, 1910, figs. 5–12). Length 10 mm

Rostrum small, down-turned, not visible in side view. Carapace soft, with anterior angle pointed. Abdominal somites rounded dorsally. Telson broad, with very small median indentation and 7+7 spines; margin fringed with spinules.

Eyes large, sessile, with black retinal pigment, the eyeball orange-red except round a dorsal colourless spot.

Labrum with small anterior spine.

Antennule with unsegmented peduncle and a seta in place of inner branch. Antennal scale broad, little more than twice as long as wide, with small apical spine; endopod less than half length of scale, with one apical seta Mandibles with undifferentiated blade and very small rudiment of palp. Maxillule has inner lobes without spines and endopod two-segmented, with two long apical setae. Maxilla with four distinct inner lobes, the basal lobe with two small setae; endopod large, not distinctly segmented, with seven setae in all; exopod large, with seven marginal setae and one very large seta on proximal lobe. Maxillipede 1, endopod of three segments, the long distal segment not distinctly divided; basis long with few setae; exopod with five setae in all; epipod small. Maxillipede 2 with epipod. Maxillipedes 2 and 3 with setose exopods; the setae are broken, and it is doubtful if there are two or three apical setae. Legs 1–5 rudimentary, biramous, the exopod on leg 5 small. Five pleurobranchs present. Luminous organs on leg 5 and pleopods 1 and 2 only. Pleopods small, bilobed. Uropods visible under skin.

Stage 2. Fig. 5, *h–k*. Length 10·5 mm.

Abdominal somites 3 and 4 with small dorsal point. Telson one and a half times as long as wide at end, with 8+8 spines,

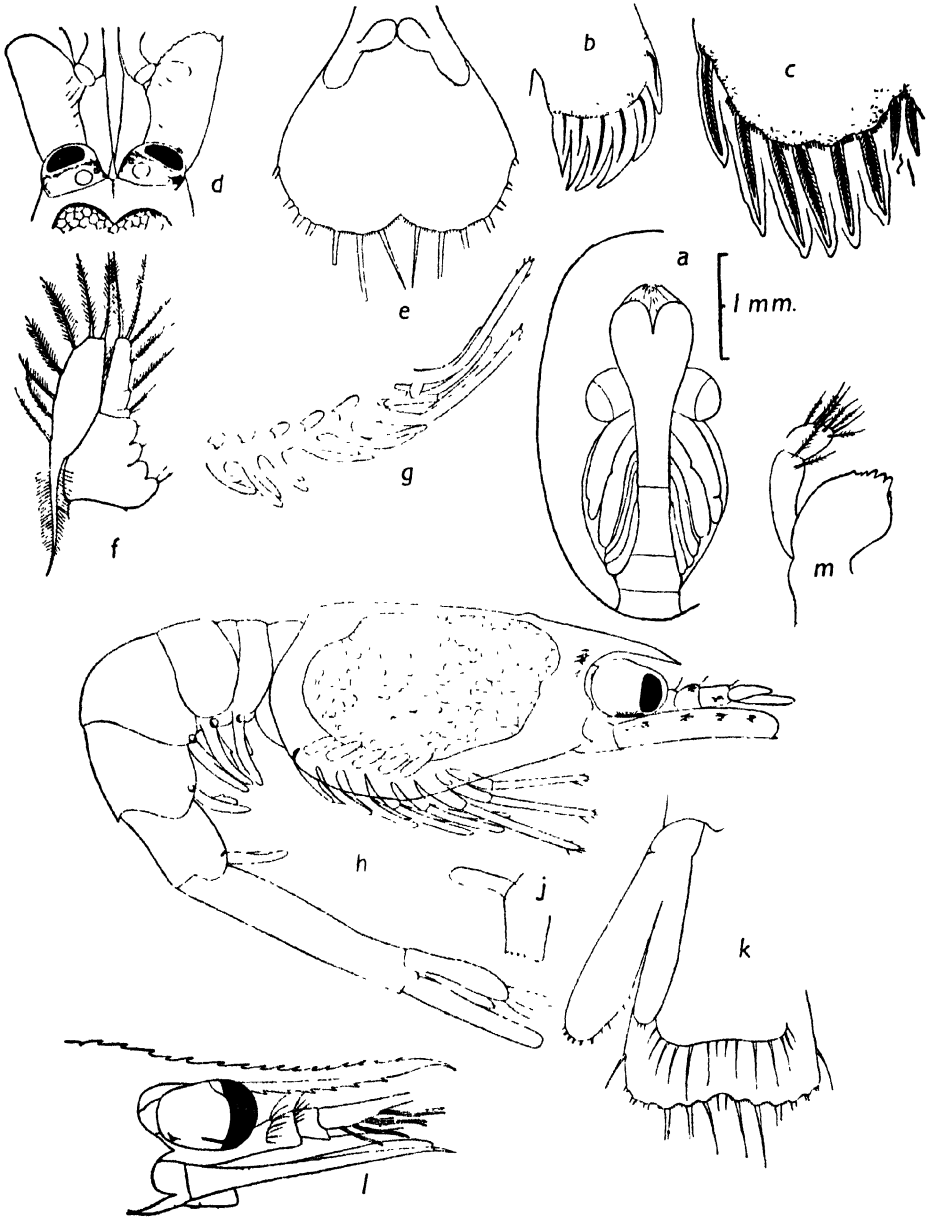

FIG. 5.—*Systellaspis debilis*. *a*, egg with embryo ; *b*, early embryonic telson ; *c*, embryonic telson just before hatching (by M. V. Lebour) ; *d–g*. Stage 1 : *d*, head and antennæ ; *e*, telson ; *f*, maxilla ; *g*, maxillipedes and legs ; *h–k*. Stage 2 : *h*, stage 2 ; *j*, mandible ; *k*, telson ; *l–m*. Stage 4 (*Discovery* Station 281) : *l*, head ; *m*, mandible.

Peduncle of antennule of three segments ; flagella stout, about as long as last two segments of peduncle. Antennal flagellum as long as scale, with basal segment distinct, and no apical seta. Mandibular palp long, unsegmented.

Maxillule and maxilla unchanged except that exopod of the latter has thirteen setae. Exopod of maxillipedes 2 and 3 with six setae. Legs larger, but very little changed.

Pleopods long. Uropods developed, the endopod not jointed to basis, and with rudimentary setae at end only.

Luminous organs on leg 5 and pleopods 1–4.

This stage, with free uropods, corresponds to the normal stage 3. No stage intermediate between this and stage 1 has been seen, and it has to be assumed that the conclusion, founded upon study of the embryonic telson, that stage 1 is passed through in the egg, is confirmed.

Stage 3. Fig. 6, *d–f*. Length of body 11·2 mm. Rostrum 1·72 mm.

Rostrum shorter than scale, with ten small dorsal teeth and smooth below. Under the skin can be seen ten teeth above and five below. Abdominal somite 3 with sharp posterior spine. Pleura rounded, except that of somite 5, which has a small point. Telson parallel-sided, its distal margin gently convex, with short median spine. There are two pairs of small lateral spines and 6+6 distal.

Flagella of antennule and antenna broken, but evidently long. Mandibular palp long, unsegmented. Maxillule and maxilla unchanged. Maxillipede 1 with large bilobed epipod.

Rudiments of epipods and arthrobranchs on legs 1–4.

Legs 1 and 2 chelate, the fingers unequal. All endopods segmented. Exopod of leg 4 setose, that of leg 5 without setae.

Luminous organs. Three on eye ; on propod of maxillipede 3 and carpus of legs 3–5 ; on legs 5 and all pleopods.

Pleopods large, with short setae. Uropods as long as telson, the endopod with numerous setae, the exopod with small outer spine.

The description is taken from a Bermudan specimen. Another in a similar stage from *Discovery* station 281 (fig. 6, *a–c*) differs in some details. The rostrum has six teeth below ; the shell margin is slightly serrated anteriorly ; pleura all rounded ; telson more pointed, with long median point. This appears to be the same form as is figured by Kemp. It is possible that it represents a distinct species, or that it is a stage intermediate between stages 3 and post-larval 1.

Another specimen taken at Bermuda at the same time as the one described differs in having the flagellum of the antenna little longer than the scale, and the telson slightly wider at the end, and with straight posterior margin. From the appearance of the new telson under the skin it would have moulted to post-larval. It may well be that there is individual variation in the degree of development after stage 2.

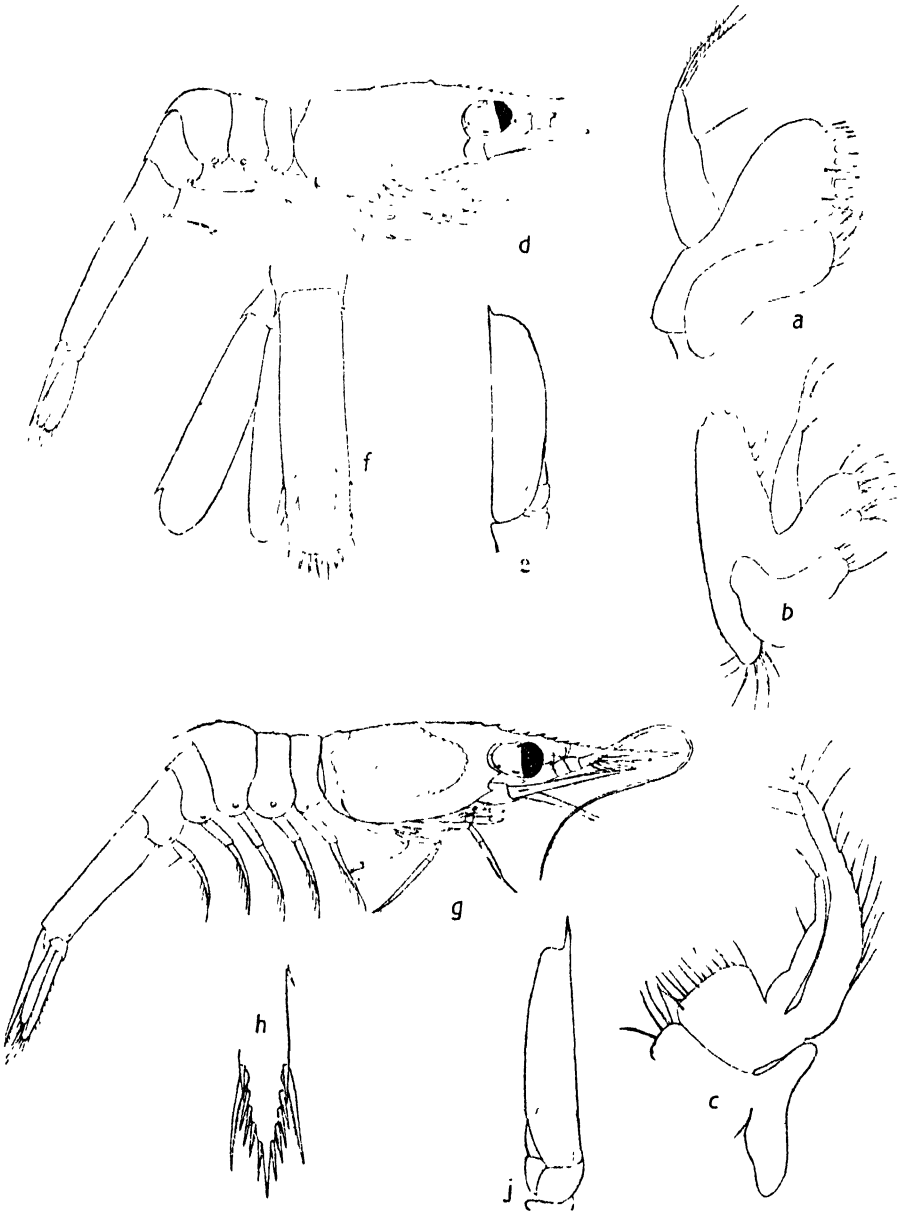

FIG. 6.—*Systellaspis debilis*. *a–c*. Stage 4 ? (*Discovery* Station 281) : *a*, maxillule ; *b*, maxilla ; *c*, maxillipede 1 ; *d–f*. Stage 3 : *d*, stage 3 ; *e*, antennal scale ; *f*, telson ; *g–j* ; post-larval 1 ; *g*, post-larval 1 ; *h*, telson ; *j*, antennal scale.

Post-larval 1. Fig. 6, *g–j*. Length 10·5 mm. Rostrum 3·5 mm.

Rostrum longer than scale, with thirteen dorsal and eight ventral spines. Carapace with subocular and pterygostomial spines, and smooth margin. Somites 3–5 with dorsal spines. Pleura of somite 5 with small point, but no spines between pleuron and dorsal spine on this or on somite 4. Telson very long and slender, tapering to a large median spine, with two pairs of lateral spines and six pairs on tapered extremity. Anal spine very small.

Eye with small papilla and three luminous organs.

Flagellum of antennule nearly as long as thorax and rostrum; peduncle with large styloccrite. Antennal scale narrow, tapering, four times as long as wide, with large apical spine. Mandibular palp large, two-segmented, with yellow setae. Mouth-parts of adult form. Legs 1 and 2 chelate, the propodus of leg 1 with three transverse rows of short spines. Ischium and merus of legs 1 and 2 with yellow setae. Leg 2 with one spine on ischium and two on merus; none on leg 1. Legs 3 and 4 merus with three spines and ischium with two. Leg 5 ischium and merus each with one spine. Exopod of all legs including leg 5 setose.

Thorax still full of yolk.

11. Hoplophorus. (Fig. 7.)

The development of this genus has not hitherto been described. Apart from one specimen taken at Bermuda the material used has been derived from the *Discovery* plankton. It is impossible to be certain about the actual species dealt with, and it may well be that the larvae of more than one species have been confused together; but I think it probable that they do belong to *H.grimaldii* Coutière. Only three specimens are sufficiently advanced to be identified with certainty, and of these two are *H. grimaldii* and one *H. spinicauda*. The following are the stations at which the material was taken :—

674.	35° 58′ S., 20° 56′ W.	280–0 m.
703.	7° 17′ N., 28° 02′ W.	358–0 m.
710.	21° 45′ S., 39° 50′ W.	294–0 m. (*H. spinicauda*).
1370.	39° 47′ S., 38° 19′ E.	113–0 m.
1591.	16° 50′ N., 18° 06′ W.	140–0 m.
1602.	17° 10′ S., 4° 28′ E.	470–300 m.
1604.	21° 35′ S., 8° 10′ E.	620–500 m.
2038.	33° 29·2′ S., 6° 37·9′ E.	1200–850 m.
2047.	24° 54′ S., 1° 44′ W.	1300–900 m.
2051.	19° 10′ S., 2° 31′ W.	990–600 m.
2055.	14° 55′ S., 03° 39′ W.	2000–1400 m. (*H. grimaldii*).
2069.	30° 47′ N., 17° 51′ W.	50–0 m. (*H. grimaldii*).

The egg and embryonic telson.

In a specimen of *H. grimaldii* of 38 mm. the eggs measure 3·2×1·9 mm. The embryos are sufficiently advanced for it to be seen that the telson has

seven spines on either side enclosed in six embryonic outgrowths as is usual among Caridea. There is, in these specimens, no evidence of a moult of stage 1 in the egg.

The Larvae.

Stage 1 (Station 2047). Fig. 7, *a–b* Length 10 mm.

Rostrum down-turned and reaching about two-thirds the length of the antennular peduncle. Carapace with pterygostomial spine and margin minutely serrate in front. Abdominal somites rounded dorsally, and with rounded pleura. Telson broad, posterior margin very slightly concave, with 7 + 7 spines.

Peduncle of antennule unsegmented, endopod represented by a small papilla with a seta. Antennal scale broad, narrowed at end and with stout apical spine, basis with large ventral spine, endopod about two-thirds length of scale, without apical seta. Labrum with small anterior spine Mandible palp large, unsegmented. Endopod of maxillule of two segments, with two apical setae; inner lobes unarmed Maxilla with four inner lobes, with a few short feathered setae; endopod of two segments, exopod large, with sixteen setae, and one very large seta on proximal lobe.

Maxillipedes 1–3 with very long exopods. Legs large, unsegmented, with non-setose exopods.

Epipods present on maxillipedes 1 and 2, and large pleurobranchs on legs 1–5.

Pleopods large. Uropods traceable under skin.

Stage 2 (Station 2047, 1602). Length 10·4 mm.

Two specimens, of which one is in process of moult and has part of the moulted skin of stage 1 attached. This stage differs very little from stage 1. The eyes are free, the telson somewhat narrower, with 8 + 8 spines, and somites 3–5 have each a small dorsal spine. Legs 1 and 2 have no trace of chelae, and the endopod of the antenna is shorter than the scale.

Stage 3 (Station 1604). Fig. 7, *c–e*. Length 10 mm. Rostrum 1·5 mm.

Rostrum stout, with eight dorsal and six ventral teeth. Telson one and a half times as long as it is wide at end, with small median point and 8+8 spines.

Antennule with long flagella (0·88 mm.). Antennal scale three and a half times as long as wide, tapering, with very large apical spine; outer margin smooth. Endopod shorter than scale, with two basal segments distinct. Mandible with large unsegmented palp. Maxillule unchanged. Maxilla with twenty-two setae on exopod, the basal lobe produced, with three setae.

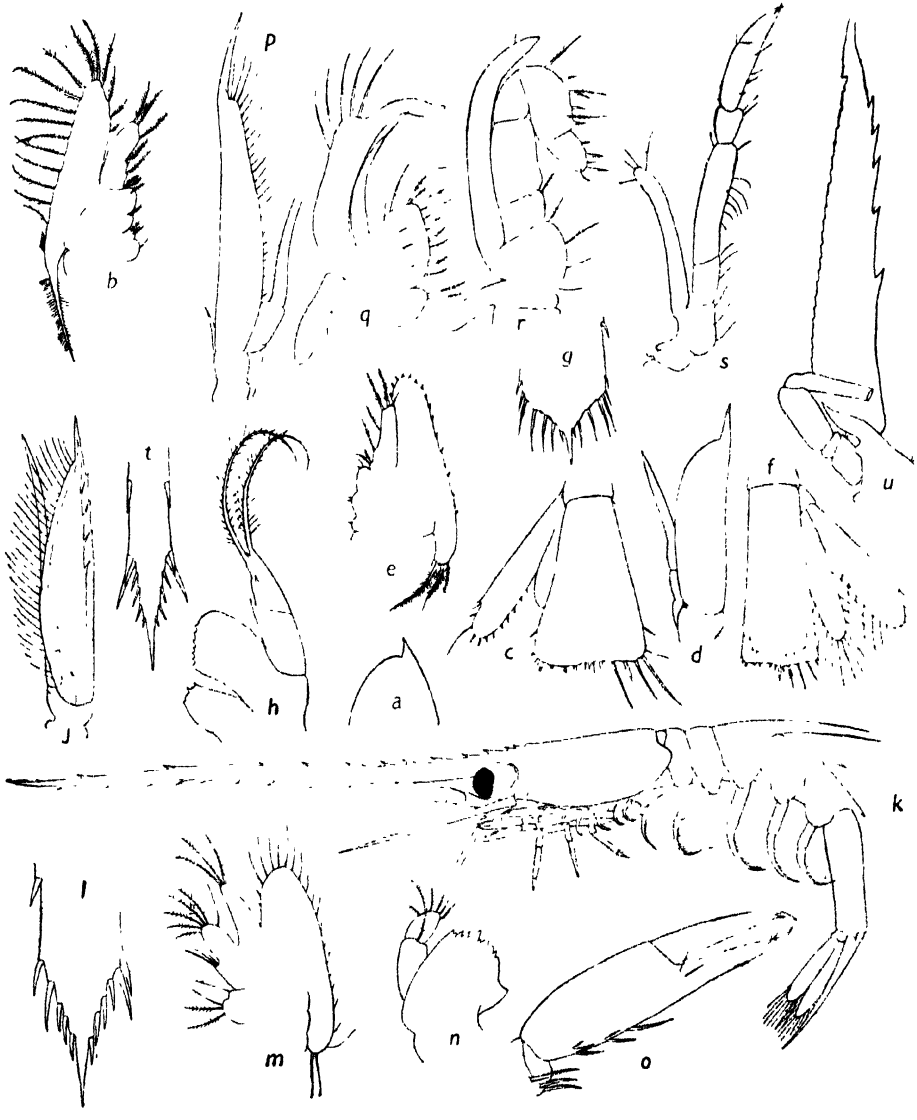

FIG. 7.—*Hoplophorus grimaldii* ? *a–b*. Stage 1: *a*, part of antennal scale; *b*, maxilla; *c–e*. Stage 3: *c*, telson; *d*, antenna; *e*, maxilla; *f*, stage 4, telson; *g–j*. Stage 5: *g*, telson; *h* maxillule; *j*, antenna; *k–s*, post-larval 1; *k*, post-larval 1; *l*, part of telson; *m*, maxilla; *n*, mandible; *o*, leg 1, chela; *p*, antenna; *q*, maxillipede 1; *r*, maxillipede 2; *s*, leg 1; *t–u*, specimen of 13·5 mm. (Station 2055); *t*, telson; *u*, antenna.

Legs all segmented, legs 1 and 2 chelate, the fingers unequal. Exopods of legs without setae, but that of leg 1 with four rudimentary setae. Pleopods large, without setae. Uropods present, the endopod not jointed to stem short, without setae.

Stage 4 (Station 1604). Fig. 7, *f*. Length 11·5 mm. Rostrum 3·3 mm.

Rostrum reaching beyond antennule, with thirteen dorsal and eight ventral spines, the proximal dorsal spines very small. Shell margin denticulate anteriorly. Dorsal spine of abdominal somite 3 reaching about half-way along somite 4. Telson 2·4 times as long as wide at end; posterior margin straight, with large median spine and 8 + 8 terminal and lateral spines. Anal spine small.

Eye with very minute papilla. Antennule without stylocerite. Antennal scale three and a half times as long as wide, outer margin smooth; endopod as long as scale. Legs 1 and 2 chelate, leg 1 with setose exopod. Exopods of legs 2–5 without setae, that of leg 5 very small.

Pleopods without setae. Endopod of uropod jointed to stem, setose.

Stage 5 (Station 1604). Fig. 7, *g–j*. Length 10·5 mm. Rostrum 4·75 mm.

Rostrum with thirteen dorsal and eight ventral spines. Dorsal spine of somite 3 as long as somite 4. Telson parallel-sided, four and a half times as long as wide; apex triangular, with large median spine and 8+8 lateral and terminal spines.

Antennular flagella 1·58 mm long. Antennal scale narrow, tapering, with outer margin smooth. A specimen from station 2047 differs in having four minute spines on outer margin and four larger ones visible under skin. Flagellum a little longer than scale. Labrum with small spine. Mouth-parts and legs unchanged, except that the exopods of legs 1–4 now have small setae.

Pleopods with short setae.

Body full of yolk.

Post-larval stage 1 (Station 674). Fig. 7, *k–s*. Length 11·5 mm. Rostrum 9·75 mm.

Rostrum with fifteen dorsal and nine ventral spines. Carapace with pterygostomial spine, but no spine under orbit. Dorsal spine of somite 3 reaching beyond somite 5. Pleura rounded, but somite 6 with small lateral spine. Anal spine small. Telson very long and slender, with two pairs of lateral spines, and six spines on either side of the median spine.

Eye with minute papilla. Antennal scale narrow, with very large terminal spine without inner hook, and outer margin smooth; basis with large ventral spine. Mandibular palp of two segments, with setae. Mouth-parts transformed,

transitional to adult form. Legs 1 and 2 equal, leg 1 with transversely arranged short spines on propod. Exopods of maxillipedes and of all legs without setae except leg 1, which has reduced setae, the exopods of leg 5 very small. Rudiments of epipods and arthrobranchs visible on legs 1–4.

No luminous organs visible.

A specimen of 12 mm. (Station 703) may be in stage 2, and has five outer spines on the antennal scale, but the terminal spine is without a hook. This hook is present in a specimen of 13·5 mm. (station 2055). Fig. 7, *t*, *u*.

Discussion.—The larvae of *Systellaspis* and *Hoplophorus* are so much alike that the two genera must be supposed to be more nearly related to each other than either is to *Acanthephyra*. The larvae may be distinguished by the shape of the antennal scale, the smallness of the exopod of leg 5, and the reduced ocular papilla in *Hoplophorus*. While luminous organs can be traced in all the larvae of *Systellaspis*, and are very distinct in those from Bermuda which are preserved in formalin, I have seen no trace of them in the specimens of *Hoplophorus*, even in one in stage 4 from Bermuda. Either they appear very late in this genus, or they are more easily rendered invisible by preservative.

The presence in the larvae of both genera of a small labral spine is a remarkable feature. This spine is found in most, if not all, Penaeid larvae, but not, so far as I know, in any other Caridea. It is also absent in Euphausiacea and *Lophogaster*, but occurs in some Mysidae.

There is an apparent difference in the number of stages: but, if the two specimens referred to on p. 106 do really represent a distinct stage, and stage 1 is really passed through in the egg, the number (five) will be the same in both.

The larvae of *Hymenodora*, as described by Stephensen, are remarkably like those of *Hoplophorus* and *Systellaspis*. There are five free stages, during which little or no growth in length occurs, and the mouth-parts remain functionless owing to the mass of yolk in the body. Apart from the absence of the long toothed rostrum they differ in form of telson in later stages and absence of dorsal spines from the abdominal somites. Stage 1 has no mandibular palp, and the endopod of the maxillule remains a small knob without setae. In these respects *Hymenodora* may be said to be less primitive than the other two genera.

The absence of setae from the exopods in the first post-larval stage of *Hoplophorus* is an example of the temporary regression of the exopods which is not unusual in the maxillipedes of Caridea at this stage. In Penaeidae the exopods may be completely lost in the post-larva and reacquired (Burkenroad, 1934, p. 136). It is possible that the same thing occurs in *Systellaspis*, and that the stage described as first post-larval is really the second, but this is unlikely in view of the fact that the body is still full of yolk. This regression of the exopods does not occur in *Hymenodora*.

The descriptions which are given here of the larvae of *Acanthephyra*, *Systellaspis* and *Hoplophorus* bring out very clearly the great differences in development which may be found in nearly related genera in consequence of an accumulation of yolk in the egg. It may be assumed that the development of *Acanthephyra* is that of the ancestral form from which all have been derived, but all those species which now have large eggs have lost almost all the structures which are definitely larval, and are concerned with larval locomotion and flotation. These are the flexure of the body with the humped third somite in which fatty matter may be stored, the long setose exopods of the legs, and, perhaps, the serration of the carapace and abdominal pleura. In contrast, development is as nearly direct to the adult form of body and appendages as is possible. The exopods are reduced and, on some legs, not functional; the endopods of the legs do not appear to be functional in larval life, and the mouth-parts are not functional at all, except insofar as they are concerned with respiration. The early appearance of the mandibular palp may also be an instance of the precocious appearance of adult characters in consequence of the mode of development.

The genera with large eggs are considered to be, judged by adult characters, on the whole more primitive than those with small eggs.

There is no connection in this group between habitat and size of egg, and it seems most unlikely that large eggs, abbreviated development, and a similar larva should have been independently acquired by each genus. The view that the mode of development has been handed on from a common ancestor implies a separation of the Hoplophoridae into groups in which there has been great divergence in development in spite of the small divergence of the adults.

3. The larval stages of *Rhynchocinetes rigens* Gordon.

By Robert Gurney.

The first and second stages in the development of *Rhynchocinetes rigens* were obtained in 1936 by Mr. Burkenroad, who has described the colour and the essential points in the structure of the larva (1939), drawing attention to the remarkable feature of its possession of an exopod on the maxillule. For this and other reasons he claims that *Rhynchocinetes* is nearly related to the Hoplophoridae.

In 1938 I was able to obtain first and second stage larvae in the laboratory at Bermuda, and to follow the subsequent stages from plankton material. The larva in the last stage had attracted my attention in 1935, and was found to be common over deep water in 1938, but its connection with *Rhynchocinetes* was not suspected until moults were obtained to the post-larval form. The great length of the antennal flagellum, which is the most striking feature of the last larva, is a character which is likely to escape notice, since it is generally broken off in the rough handling of a plankton sample.

I am indebted to Miss Lebour for a number of specimens, including post-larval stage 2, obtained by moult, which have been very helpful in establishing the sequence of stages.

Stage 1. Fig. 8, *a–h*. Length about 2·0 mm.

Rostrum long, reaching beyond antennule. Carapace margin sinuate, without marginal denticles, but with large spine at anterior angle; dorsal organ and posterior papilla small. Telson triangular, with small median hollow and 7+7 spines, of which the fourth is the longest. Antennal scale with four distal segments distinct; two outer and ten inner and apical setae. Endopod with a very long apical seta and a small seta at its base; basis with large ventral spine. Maxillule with exopod bearing three setae; endopod of two segments, bearing two and three setae respectively. Maxilla with four well-marked inner lobes; endopod large with distinct basal segment; exopod with five setae. Exopods of maxillipedes 2 and 3 with three apical setae. No leg rudiments present.

Colour.—General colour red and yellow. Diffuse orange in abdomen, tending to form a streak on either side. Red and black in somite 6 and telson.

Stage 2. Length 2·4 mm.

Stage 2 differs from stage 1 in having the eyes free, telson with 8+8 spines, and exopods of maxillipedes 2 and 3 with four apical setae. The appendages are unchanged except that the exopod of the maxillule has only one or two smaller setae. The last segment of maxillipede 3 in this and preceding stage is small, bearing two long smooth setae and a long slender spine (fig. 8, *l*).

Stage 3. Fig. 8, *j–l*. Length about 3·0 mm.

Rostrum nearly as long as antennular peduncle. Carapace without supra-orbital spine. Telson a little longer than wide (65 : 55), deeply hollowed behind, and with 8+8 spines. Endopod of antennule a small papilla, with seta. Antennal scale with two distal segments distinct, and two outer setae; basis with large spine; endopod very stout, unsegmented, nearly as long as scale, and without setae. Other appendages almost unchanged, the maxillule still with a vestige of the exopod, bearing two setae. Exopod of maxilla with seven setae. Leg 1 a large biramous rudiment; a small rudiment of leg 2.

Pleopods absent. Uropods present, The endopod small, not jointed, and with two small setae. Anal spine absent.

Stage 4. Fig. 8, *m*, *n*. Length 3·5 mm.

Rostrum shorter than antennular peduncle. Telson more than twice as long as wide (98×44), parallel-sided, deeply indented, and with 8+8 spines.

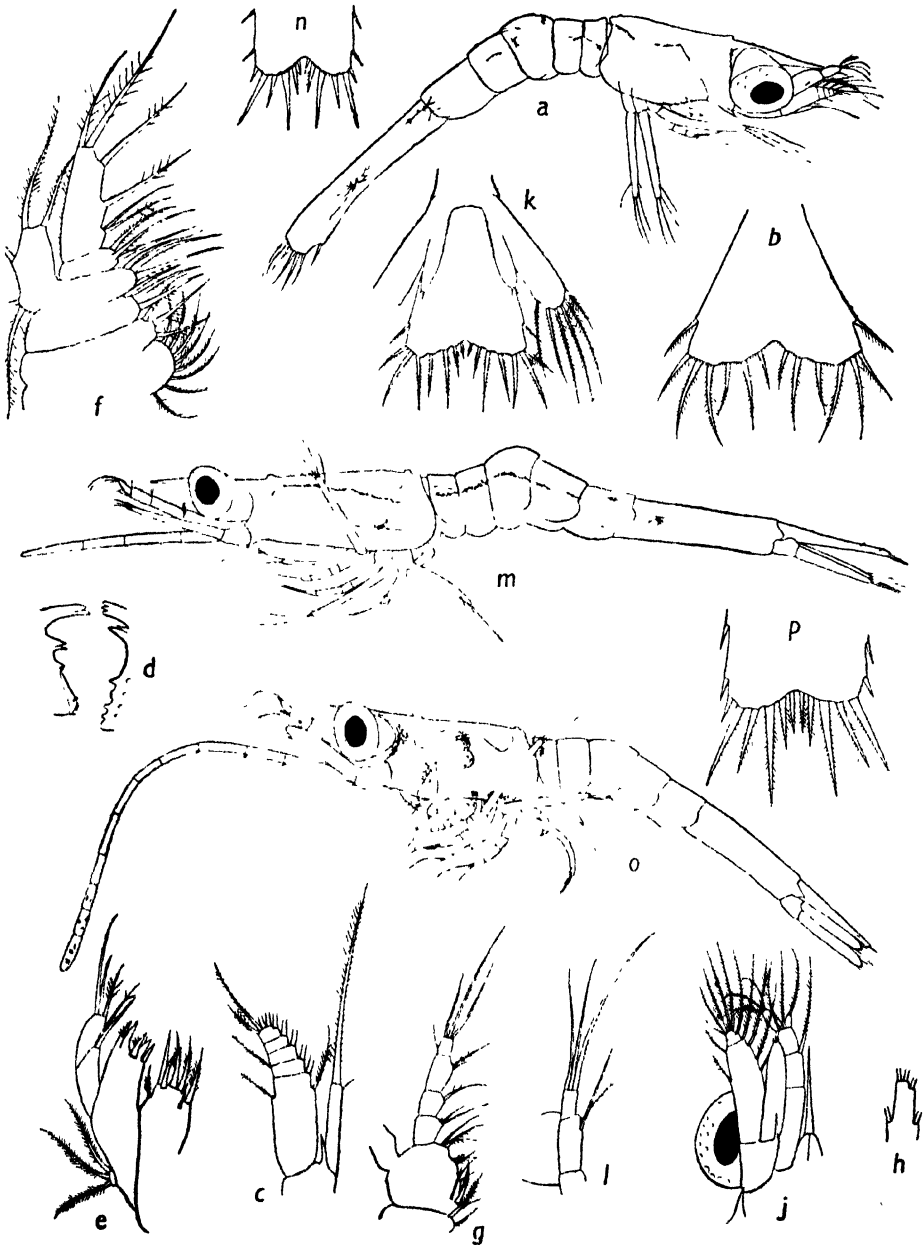

FIG. 8.—*Rhynchocinetes rigens*. *a–h*. Stage 1 : *a*, stage 1 ; *b*, telson ; *c*, antenna ; *d*, mandible ; *e*, maxillule ; *f*, maxilla ; *g*, maxillipede 1 ; *h*, exopod of maxillipede 3. *j-l*. Stage 3 : *j*, head and antennae ; *k*, telson ; *l*, end of maxillipede 3. *m–n*. Stage 4 : *m*, stage 4 ; *n*, telson ; *o–p*. Stage 5 : *o*, stage 5 ; *p*, telson.

Anal spine present, blunt. Antennule with very small unsegmented endopod. Antennal scale unsegmented, with apical outer spine ; endopod twice as long as scale, with four segments. Maxillule with minute outer papilla without setae. Exopod of maxilla with eleven setae. Maxillipede 1 with rudiment of epipod. Leg 1 with exopod bearing six setae ; endopod not distinctly segmented. Leg 2 a biramous rudiment. Pleopods absent. Uropods nearly as long as telson, the endopod jointed and with several setae.

I have only one specimen of this stage, and I find that it has a small, but quite distinct, spine at the anterior end of the labrum. This spine is evidently homologous with the labral spine of the Penaeidae, and the spine found in *Systellaspis* and *Hoplophorus*. I have, however, been unable to find it in any other specimen of *Rhynchocinetes*.

Stage 5. Fig. 8, *o*, *p*. Length 3·0–3·5 mm.

Telson more slender, two and a half to three times as long as wide. The posterior margin may be straight or slightly indented. Antennule unchanged, but with long sharp ventral spine on segment 1. Antennal endopod developed into a flagellum nearly as long as the body and slightly thickened at the end. Maxillule without trace of exopod. Exopod of maxilla with twelve setae, without proximal extension. Legs 1 and 2 developed, the endopods of five segments, the last segment bearing a long slender spine and two setae like the maxillipedes ; exopods with eight and six setae respectively. There is a rudiment of leg 3. There are no gill rudiments. Pleopods absent.

It would seem that stage 6 is not represented in my material.

Stage 7. Fig. 9, *a–d*. Length 4·75 mm. without rostrum (·7 mm.).

Rostrum reaching end of segment 2 of antennule, with one small dorsal spine. There is also a small spine on the carapace in front of the dorsal organ, and a small supraorbital spine. Telson more than three times as long as wide, wider in front, the posterior margin convex. There are three pairs of lateral spines and 6+6 terminal. Branches of antennule slightly longer than last segment of peduncle, unsegmented. Antennal flagellum broken off. Exopod of maxilla with numerous setae, and slender proximal process.

Maxillipedes 1 and 2 with epipods, but gills absent. Leg 4 developed, the endopod of five segments, and exopod with six setae. Leg 5 a large rudiment, with rudimentary exopod. Pleopods absent.

Stage 8. Fig. 9, *e*, *g*. Length 5·3 mm. Rostrum ·75 mm.

Rostrum reaches end of segment 2 of antennule. There is one dorsal tooth

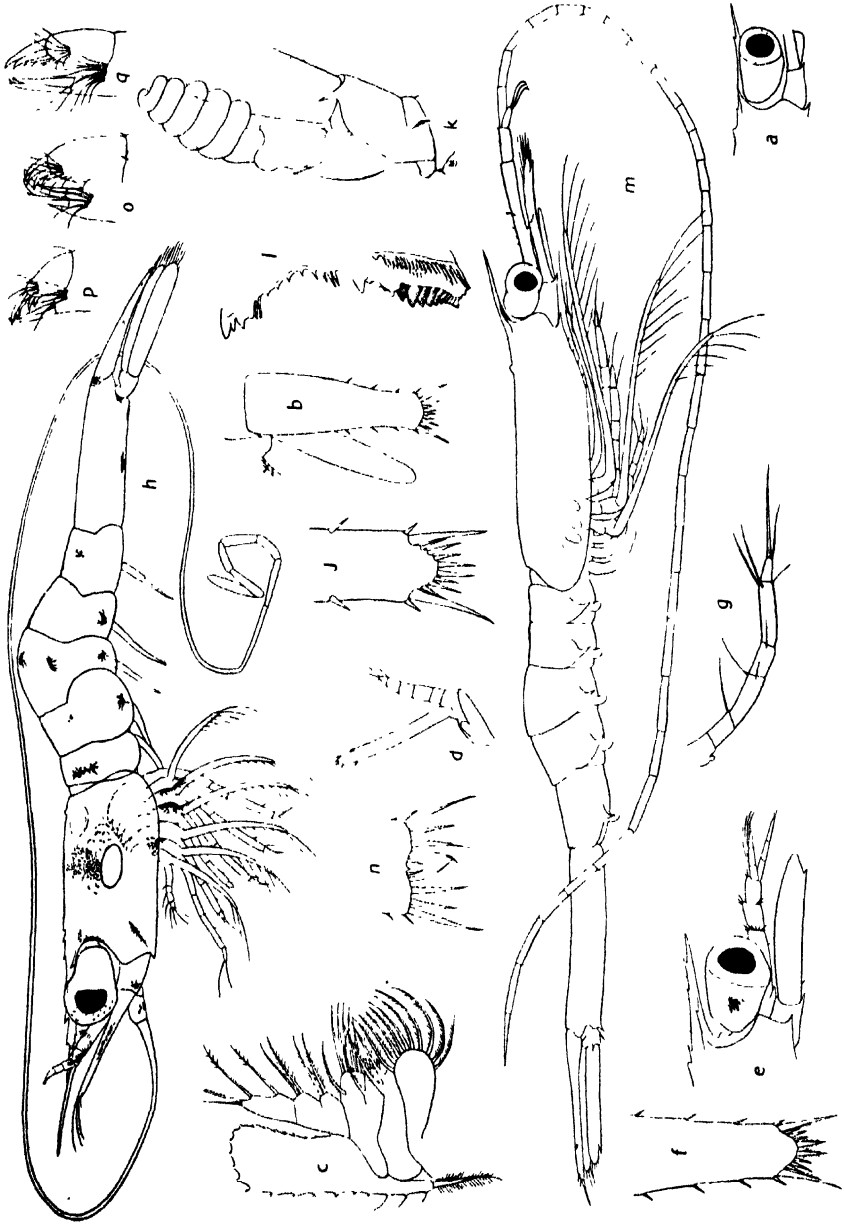

FIG. 9.—*a–d*. Stage 7: *a*, head; *b*, telson; *c*, maxilla; *d*, legs 4 and 5. *e–g*. Stage 8: *e*, head; *f*, telson; *g*, leg 5. *h–l*. Stage 10: *h*, specimen of 7·2 mm.; *j*, telson; *k*, antenna; *l*, mandible; *m*, larva of unknown genus with long antennular flagellum. *Discovery* station 278; *n*, telson of same. *o–q*. Post-larval 2: *o*, chela, leg 1; *p*, chela, leg 2; *q*, chela, leg 2, adult female.

on the rostrum and one just behind it on the carapace, but no ventral teeth. Telson nearly four times as long as wide (121 × 34), with three pairs of lateral spines and six terminal.

Leg 5 developed, the endopod segmented and setose, with distinct rudiment of exopod.

Small pleopod buds present on somites 2–5.

Stage 9. Length 6·05 mm. Rostrum ·8 mm.

Rostrum reaching between segments 1 and 2 of antennule, with two small dorsal teeth. Telson of the same form, but very convex at end; the spines the same. Antennule with small stylocerite; the branches about as long as last two segments of peduncle, of three segments; segment 1 with large ventral spine. Flagellum of antenna 5·5 mm. long, scarcely at all swollen at end. Exopod of maxilla very broad in front, and with long proximal process. Legs all developed, leg 5 with minute rudiment of exopod. Epipods present on maxillipedes 1–3, and pleurobranchs on legs 1–5, decreasing in size from leg 1 backwards. Arthrobranchs absent. Legs 1 and 2 without trace of chelae. Pleopods small, bilobed.

Stage 10. Fig. 9, *h–l*, 10, *a–e*. Length 7·3 mm. Rostrum 1·12 mm.

Rostrum reaching to, or beyond, end of antennular peduncle, with no ventral spines and two dorsal, in addition to one on carapace in front of dorsal organ. Carapace with small supraorbital spine. The thorax seems always to contain, in life, a large central oil globule. Telson about four times as long as wide, with same spines as before, but the apex more convex.

Antennule stout, with rudimentary stylocerite and ventral spine on segment 1; exopod shorter than endopod, of three or four segments; endopod slender, with about six segments. Antennal flagellum much longer than body, the last six segments somewhat swollen and peculiarly bent. Mandible with small unsegmented palp.

Maxillule with proximal lacinia very broad; endopod slender, of two segments. Exopod of maxilla broad in front, the proximal extension widening at end. Maxillipede 1 with large bilobed epipod. The epipod of maxillipede 2 has a small lobe representing the podobranch. Legs all fully developed, but legs 1 and 2 without trace of chelae. Leg 5 without exopod. Pleopods large, with small setae.

I am much indebted to Miss Lebour for the following note on the colouring and antenna of the last larva.

The last larva is a uniform, very pale yellow all over, and very transparent, and there are patches and bands of red on the body. The abdominal somites 1–5 have each a band of red, and 6 has a large red patch at the posterior end. There are red patches on the middle of the telson and on the tips of the uropods,

at the base of the antennules and antenna, on the eye just beyond the stalk, on the thorax anteriorly and in the centre, and on the bases of the legs. The antennal flagellum is enormously long, nearly four times the length of the body. It is held straight out in front of the body, and is coloured red at intervals along its whole length, red and colourless parts alternating at about equal distances.

Several larvae of this stage and of this size moulted to post-larval, and there is no doubt this is properly to be regarded as the last larval stage ; but I have numerous specimens which greatly exceed this size and yet show no marked difference in structure. They may be as much as 14 mm. long without rostrum, and the only distinct difference is that the rostrum may have an additional dorsal spine and one or two very small ventral spines. There may also be one more spine on the carapace, making five dorsal spines in all. The telson remains the same, except that it becomes more slender and the end between the two large spines is more prominent (fig. 10, *e*). In all these large specimens the antennal flagellum is broken off, but I have seen two complete detached flagella which may have belonged to specimens in the same plankton sample. These flagella measured 34 and 36 mm. The segments are covered with minute spinules, and the last three are very much dilated and apparently freely moveable on their narrowed bases (fig. 10, *d*).

It would seem that, on reaching stage 10, larval life may be continued for quite a long period, with a succession of moults involving no great change except in the growth of the antennal flagellum.

I have had two moults of stage 10 to a larger larva of the same general stage. In one of these the antennal flagellum measured 18·5 mm., or only about half the length of the flagellum which the oldest larva appears to have.

So far as I am aware, the only Caridean larva having such a remarkably long flagellum is a form of *Eretmocaris* in which, with a body-length of 9 mm., the flagellum measured more than 31 mm. (Gurney, 1937, p. 375). The only other comparable case is that of a larva of 7 mm. from the *Discovery* material (Station 278) in which the antennule has the inner flagellum much longer than the rest of the body—about 11 mm. (fig. 9, *m*, *n*). No doubt the flagellum has a suspensory function like that of *Sergestes*. When broken off it regenerates as a closely coiled spiral, just as it does in *Sergestes* (fig. 9, *k*).

Post-larval stage 1. Fig. 10, *f–j*.

Specimens of this stage were obtained both by moult and from the plankton. They do not show a range of size at all comparable with that of the last larva, and indeed rarely exceed 8 mm. There is some variation in the degree to which the exopods of the legs are reduced, and there may be some corresponding differences in the development of the mouth-parts, but this has not been shown in the specimens dissected. It would seem that the mouth-parts, as is often

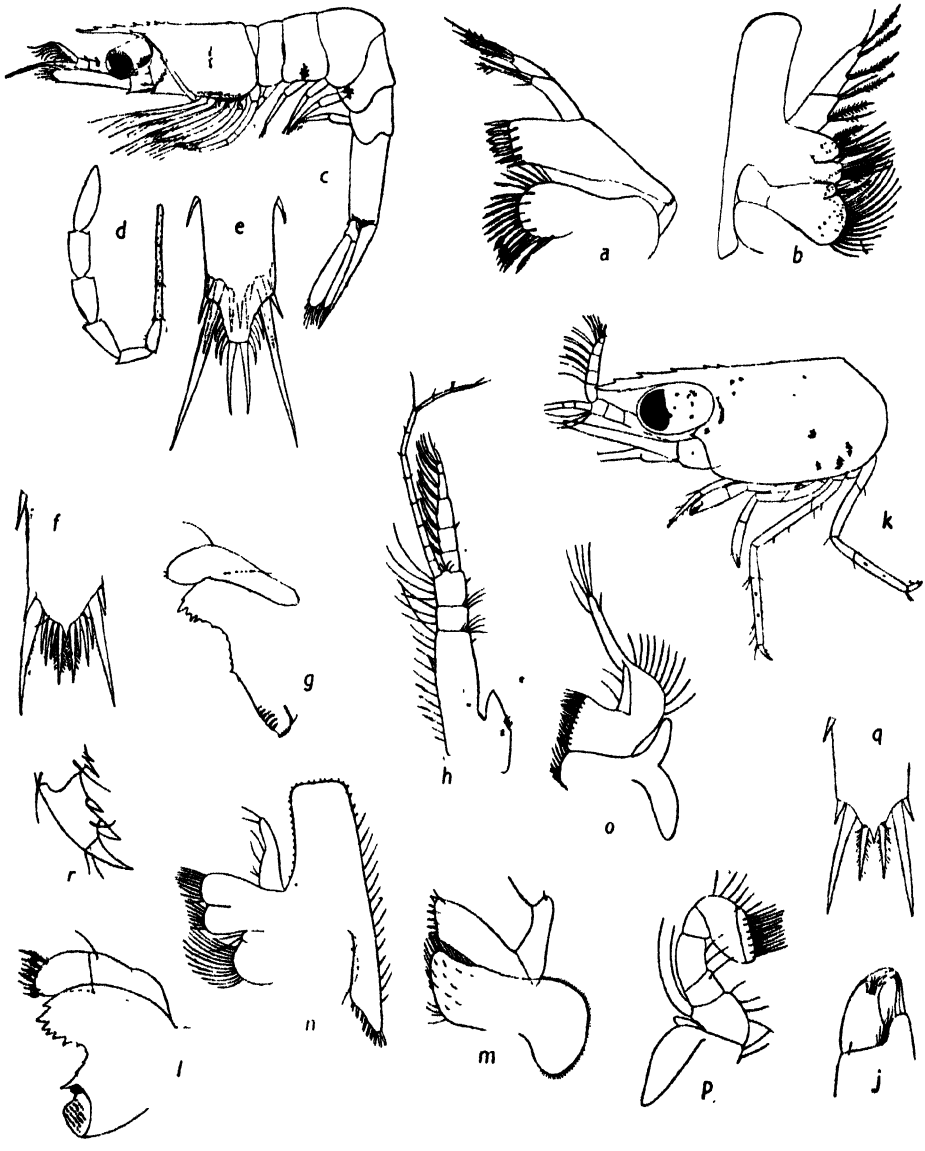

FIG. 10.—*a–b*. Stage 10: *a*, maxillule; *b*, maxilla. *c–e*. Stage 10, specimen of 9·7 mm.: *c*, stage 10; *d*, part of antennal flagellum believed to belong to it; *e*, telson. *f–j*. Post-larval Stage 1: *f*, telson; *g*, mandible; *h*, antennule; *j*, leg 1, chela; *k–r*. Post-larval 2. *k*, thorax; *l*, mandible; *m*, maxillule; *n*, maxilla; *o*, maxillipede 1; *p*, maxillipede 2; *q*, telson; *r*, leg 3 dactyl.

the case in Caridea at this stage, are not fully functional, and the setae of the exopods of maxillipedes 1 and 2 are temporarily reduced. The following description is from a specimen moulted in the laboratory.

Length 7·7 mm. Rostrum 1·25 mm.

Rostrum reaching end of peduncle of antennule, with three dorsal and two minute ventral spines. Carapace with two dorsal spines in front of the dorsal organ, small antennal and pterygostomial spines, but no supraorbital spines. Thorax with a pair of sternal spines between the bases of leg 5. Pleura of somites 3–5 with very small point, and lateral process of somite 6 pointed. Anal spine large.

Telson about four times as long as wide, with three pairs of lateral spines and 6+6 terminal; distal end produced between the two large spines and ending in a small point.

Antennule with ventral spine and large stylocerite; outer flagellum of six segments, about two-thirds length of peduncle; inner flagellum longer than peduncle. Antennal flagellum now not much longer than body and of normal slender form. The basal segment of it has an inner spine, and is quite clearly a portion of the basis, and not properly part of the flagellum.

Mandible with molar and incisor parts not marked off by a depression; the incisor part with a series of five or six large anterior teeth, and a series of small teeth between it and the molar part; palp large, but unsegmented and with few setae. The other mouth-parts have assumed the adult form and differ from those of stage 2 only in having fewer setae and a more or less undeveloped appearance. Maxillule with exite, but very much smaller than in stage 2, and without fringe of hairs. Maxillipede 1 having coxa quite without setae, and apical setae of exopod much reduced; endopod longer than in stage 2. Maxillipede 2 has epipod with rudiment of podobranch, but it is smaller than in stage 2. Legs 1–4 with small epipods, but no arthrobranchs. Legs 1 and 2 chelate and resembling those of the adult, but with fewer spines. In both legs the propodal process (fixed finger) is barely half the length of the dactyl, and bears two large spines. Carpus of leg 1 little more than half length of chela, and a little shorter than the chela in leg 2. Legs 1–4 with very long exopods without setae.

Post-larval 2 (by moult from stage 1). Fig. 10, *k–r*. Length 8·0 mm. Rostrum 1·3 mm.

Rostral spines as before, but in this specimen with four minute ventral spines. Carapace with pterygostomial angle rounded. Abdominal somites 4 and 5 apparently lacking the posterior lateral spines of the adult.

Antennule as in stage 1, but inner flagellum longer (2·8 mm.). Antennal flagellum about 9 mm. long. Mandible approaching adult form, with deep hollow between incisor part, with seven teeth, and molar part; palp with distal segment distinct, but proximal part undivided. Maxillule with very large

exite fringed with hairs. Proximal lobe of maxilla very much shorter than distal lobe, and distinctly divided into a large proximal part and a very small distal lobe. In the adult there is still a lappet representing this small distal lobe. Maxillipede 1 with large bilobed epipod. Maxillipede 2 as in adult, the epipod with a branch representing podobranch. Maxillipede 3 with bifurcated epipod and long setose exopod. There are two rudimentary arthrobranchs on maxillipede 3, but none on the legs. Legs 1–4 with trace of exopod in specimen described, but leg 1 only has it in specimen figured (fig. 10, *k*). Legs 1 and 2 differ little from those of stage 1. Legs 3–5 with dactyl short, bearing three strong spines.

Telson differing from stage 1 in having lost three pairs of terminal spines. As in the adult there are now only six terminal spines.

I have seen no specimens more developed than this, and consequently none in which the rostrum shows the least resemblance to that of the adult.

The systematic position of *Rhynchocinetes*.

Milne-Edwards regarded *Rhynchocinetes* as close to *Hippolyte*, and Ortmann (1890) also treated it as a primitive form of Hippolytid. Rathbun (1906) placed it between the Crangonidae and Lysmatidae, while Borradaile (1907) included it in his superfamily Palaemonoida. Balss (1927) also included it in the Palaemonoida, between Hippolytidae and Palaemonidae. Burkenroad (1939), mainly on the ground that the larva has an exopod on the maxillule, has argued for its transference to the group Hoplophoroida. This conclusion is, I believe, the correct one, but, before discussing it, it is necessary to define to some extent the limits of the Hoplophorid group. Burkenroad follows Balss in including the families Atyidae, Hoplophoridae, Nematocarcinidae, Campylonotidae, and Disciadidae, but adds also Gonatonotidae. If all these families are included it is difficult to find any common characters which would separate the group as a whole from the Pasiphaeoida on the one hand and the Pandaloida on the other. There appears to be no reason, apart from the possession of exopods on some of the legs, for including *Nematocarcinus*, which Alcock (and Balss himself in 1925) regarded as a Pandalid. The relationship of *Gonatonotus* (*Eugonatonotus* Chace) is obscure. Its mouth-parts show no obvious affinity with the Hoplophoridae and the vestigial exopods on the legs, apart from the fact that there is one on leg 5, do not of themselves determine its position. *Campylonotus* seems to bear very much the same relation to typical Hoplophorids as I hope to show *Rhynchocinetes* does.

So far as adult structure is concerned, very little evidence can be obtained for deciding the position of *Rhynchocinetes*, but the mandible is, in my opinion, distinctly of the Hoplophorid type. It is characteristic of the Hoplophoridae, Pasiphaeidae, and some Atyidae (*Xiphocaris*) that the incisor portion is a flat blade armed with a series of large teeth, that the molar portion is not separated

from the incisor portion by a deep hollow, and that it may be reduced to insignificance. In most Pasiphaeidae it is flattened out and merges with the incisor portion, being itself armed with teeth but little different from those of the incisor blade. In *Rhynchocinetes* the incisor part is a blade, exactly the same as that of a Hoplophorid, with six teeth. It is separated from the molar part by a deep hollow, but, in the first post-larval stage this hollow is much less marked, and it is bridged by a series of small teeth which continue the series of incisor teeth. There is, in fact, no real difference between this mandible as a whole, with its three-segmented palp, and that of *Acanthephyra* for example.

Another point of resemblance to which I think attention has not been drawn is the presence on the maxillule of a large exite. A precisely similar exite is characteristic of most Atyidae, and it can be traced, though much reduced, in *Systellaspis* and, no doubt, in other Hoplophoridae. So far as I am aware, it has not been seen in any Caridea outside the Hoplophoroida. There seems to be no character of the adult *Rhynchocinetes* which would exclude it from the Hoplophoroida except the absence of exopods from the legs. This is a character of very doubtful significance. Their absence in *Campylonotus* has not prevented its inclusion with the Hoplophoroida, and exopods are by no means universal among the Atyidae.

The larva contributes additional evidence for the placing of *Rhynchocinetes* among the Hoplophoroida. As Burkenroad has pointed out, the presence of an exopod on the maxillule is a very primitive feature, since such an exopod is only known, among Caridea, in *Xiphocaris* and *Caridina*. As Miss Lebour has shown that the larva of *Acanthephyra* does not have this exopod, it is clear that the larva which I have described as *Acanthephyra* (?) (1924 *c*, p. 108, fig. 37), which has an exopod, does not belong to this genus. There can be little doubt that it is actually *Rhynchocinetes*.

A very remarkable feature of the development of *Rhynchocinetes* is the appearance of a rudimentary exopod on leg 5. Although this exopod disappears again before the close of larval life, it is unmistakable proof that the genus has been derived from the Hoplophorid group in which alone leg 5 has, either in larva or adult, retained an exopod.

Although a labral spine has only been seen in a single specimen, it is fair to draw attention to the fact that this spine, which is characteristic of the Penaeidea, is only known to occur in *Systellaspis* among Caridea.

The form of the telson, with its distal prominence, recalls that of certain species of the larval genus *Caricyphus* which Coutière (1905 *d*, p. 25) has claimed to be primitive. As the parentage of these larvae is not yet certain this point has not much weight.

Lastly, the appearance of the mandibular palp before the close of larval life (in stage 10) may be regarded as a point of resemblance to Hoplophoridae. As Miss Lebour has shown, this palp does not appear as early as Coutière supposed ;

but it is most unusual for it to appear at all during larval life in Caridea other than Hoplophorids.

The comparative rarity of early larval stages and the abundance of late ones seems to show that the early stages may be passed through rapidly and that a prolonged period of planktonic life ensues during which growth without much structural change takes place. It has been possible to distinguish ten "stages" during which a size of about 7 mm. is reached, and at this point transformation to post-larval may take place; but the size may be doubled without this transformation. Miss Lebour finds in *Acanthephyra* that there may be a number of stages between the seventh of 7 mm. and the final stage of 12 mm. at which she obtained a moult to post-larval, and the evidence from the very large larvae of unknown parentage taken by the *Discovery* shows that a prolonged period of larval life is characteristic of oceanic Caridea. In some cases it may, apparently, be continued even up to sexual maturity, since I have seen larvae with rudimentary male appendix on pleopod 2. In spite of the littoral habitat of the adult, *Rhynchocinetes* has a larva which may be said to be of oceanic type, which is consistent with the postulate that the genus is derived from a Hoplophorid stem.

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4. *Eretmocaris dolichops* and a new closely related species.

By Marie V. Lebour.

Gurney (1937 *b*) regards the larval genus *Eretmocaris* of Bate as a composite one, and among the larvae described selects two (A VI and A VII) which stand apart from the others in several characters. He identifies A VI with Ortmann's *Eretmocaris dolichops* (1893, p. 79, pl. v). Neither in Ortmann's specimen nor Gurney's were the legs beyond the second pair present. This larva is fairly common in Bermuda in the outside waters and moults were obtained in which the legs were in perfect condition, and some of these were slightly older than any known before. The moults, however, hardly differed from one another, and in no case was a post-larva obtained. Dr. Gurney also had moults without change. Besides *E. dolichops* one specimen only was found of a new form (X) with jointed eye-stalks, evidently closely related, but having large paddles on legs 3–5. Moults were also obtained from this larva, but with very little difference in form, and again no post-larva.

ERETMOCARIS DOLICHOPS Ortmann. (Fig. 11, *a–d.*)

Gurney (p. 372 describes and figures one specimen, 11·6 mm. in length. The largest from Bermuda, from a moult, measured 13 mm. It agrees with his description, but is slightly further advanced, the antennular and antennal flagella reaching beyond the eye, and the telson ending in eight instead of ten spines (in a younger stage there are ten). The mouth-parts are similar and legs 1 and 2, although these legs are slightly longer. Gurney surmises that leg 4 has an exopod and leg 5 has none, and is not enlarged, which proves to be correct. The mandible is undivided, but is slightly twisted, and has the cutting and grinding parts distinct with long and sharp teeth in between. Legs 3–5 are very long, as long as the body without the telson, and of almost equal length. The propodus is long and swollen, although not paddle-shaped, and the dactyl small and simple. There are very long exopods with numerous setae on legs 1–4 and epipods beginning to be formed, conspicuous pleurobranchs, but no arthrobranchs. There is an appendix interna on the pleopods. The carapace has deep grooves dorsally. The telson is straight terminally with eight spines, the outer pair being much the largest, and there are no lateral spines. A younger specimen had the end of the telson slightly convex with ten spines. In none of the specimens was there a small spine outside the largest pair. The pleopods are setose.

Colour.—The larvae were very transparent, having a patch of red with yellow behind it in the centre of the thorax, red lines anteriorly on abdominal somites 2–4, and a pinkish patch between somites 3 and 4. The propods of legs 3–5 are deep red, the colour formed from many chromatophores.

ERETMOCARIS X. (Fig. 11, *e–h.*)

This specimen also measured 13 mm. in length when captured a few miles off Bermuda, 300 metres depth. The eye-stalks are jointed and very long, the antennular and antennal flagella reaching well beyond them. The antennular peduncle has three segments, but otherwise the antennule and antenna are similar to *E. dolichops*, as are also the mandible, maxillule, maxilla, and first and second maxillipedes. The third maxillipede, however, differs in being armed on its distal half with very long hairs. The rostrum and dorsal organ are similar to *E. dolichops*, there are deep grooves on the carapace of a different pattern and antero-ventrally there are three teeth. There are no supra-orbital spines. Legs 1 and 2 are similar to *E. dolichops* but longer, the propodus of 1 being longer than that of 2. The second leg reaches beyond the antennal scale. Legs 3–5 are long, nearly as long as the body, and are of nearly equal length, and end in broad paddles with marginal spines, the ischium and merus are separate. The dactyl is very small. They are armed with very long hairs. Legs 1–4 have long exopods with numerous setae, the exopod of the third maxillipede being short. The pleopods are setose. The telson is straight terminally and is armed with eight spines, the outer one much the longest. There are no lateral spines and no small spines outside the large pair. The

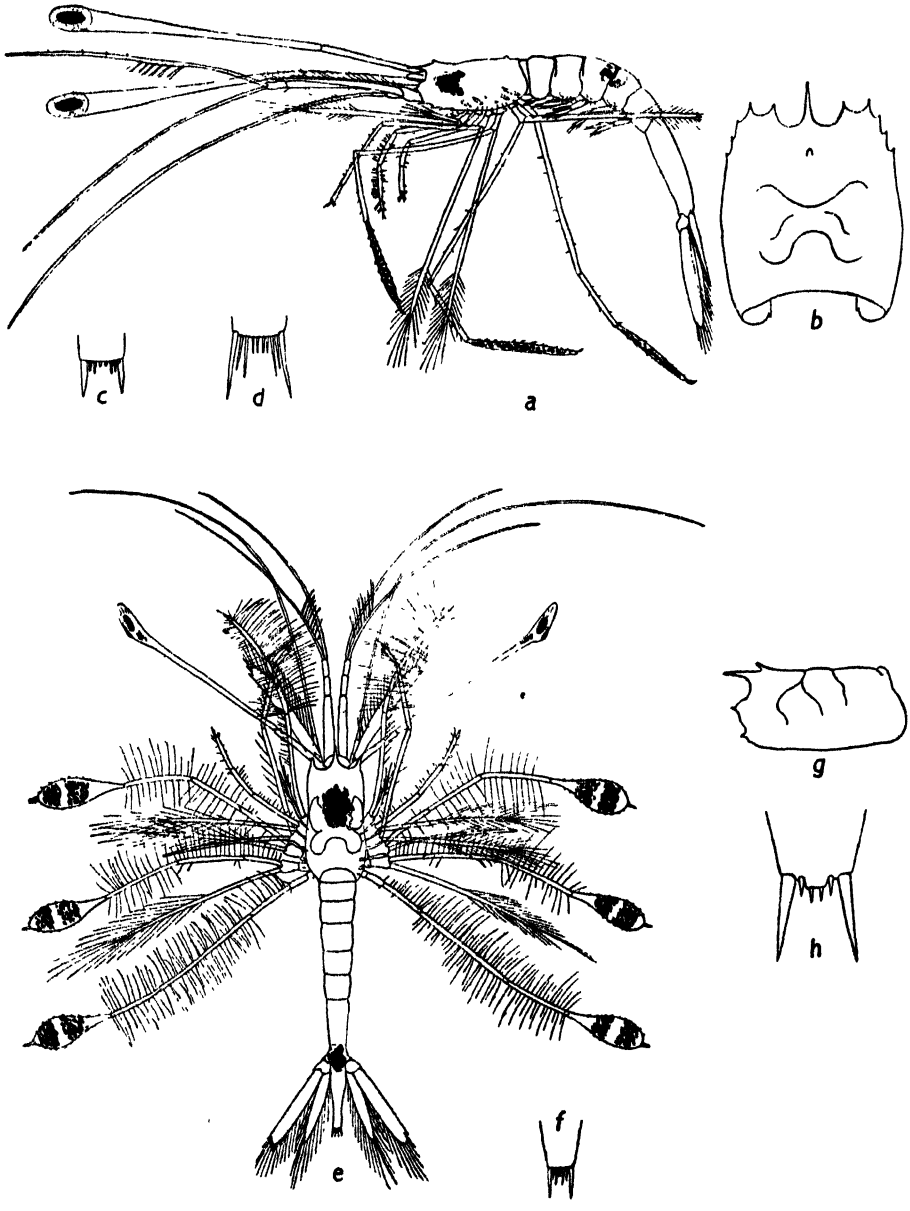

FIG. 11.—*a–d, Eretmocaris dolichops.* *a*, larva 13 mm. long; *b*, carapace; *c*, telson; *d*, telson of younger stage. *e–h, Eretmocaris*, X. *e*, larva 13 mm. long; *f*, telson; *g*, carapace of later stage; *h*, telson of same.

abdominal somites are rounded as in *E. dolichops*. Epipods are beginning to be formed on legs 1–4. This specimen moulted four times, and then died when still in the larval stage. The moults were very similar, but showed still longer legs, and the carapace in the last moult had lost the antero-ventral teeth and had an antennal and a pterygostomial spine. The telson now ends in six spines, the outer pair being situated higher up than the other and the intermediate pair slightly more dorsal than the inner pair. In the cast skins the mouth-parts were similar to those of *E. dolichops*.

Colour.—The larva is very transparent, with red on the eyes and just behind the cornea, a large red patch dorsally in the centre of the carapace and at the end of the sixth abdominal somite running on to the telson. There are two broad red bands on the paddles of legs 3–5.

The following dates show the moults :—4. 6. 39, 10. 6. 39, 15. 6. 39, 25. 6. 39. Dr. Wheeler, Director of the Bermuda Biological Station, kindly cared for this specimen after the first three moults until it died.

These two species are obviously closely related, species X being slightly more advanced than the last stage known in *E. dolichops*. The fact that they still retain the larval mouth-parts, and that probably the rostrum is not of the adult form seem to indicate that they have not yet reached the end of their larval state, and that the post-larval stage will not be attained before more moults have taken place. They are obviously deep-water larvae, being taken from 100 to 300 metres and more. No very young stages have ever been seen.

One cannot place these larvae with any certainty, but the adult must be a deep-water form with long legs. It is certain that the two species are closely related, having the following important points in common :—

They have very long eye-stalks with a joint.

There are no supra-orbital spines.

The legs are very long, the third to the fifth legs being of about equal length and the fifth not enlarged.

Epipods are present on legs 1–4.

Legs 3–5 have the propodus enlarged.

The telson has no lateral spines, is straight terminally (except in the latest stage of X, where the end is narrowed), and ends in eight or six spines, the outermost pair being much the largest, and having no small spines just outside which are present in all the *Eretmocaris-Lysmata* group.

On the other hand, they agree with the late stages in the *Eretmocaris-Lysmata* group as described by Gurney in the form of legs 1 and 2, in having long and powerful exopods on legs 1–4 and in the mouth-parts, in the tendency to enlarge the propodus of legs 3–5 (in the *Eretmocaris-Lysmata* group it is usually only leg 5 ,but in Species A IV all three are enlarged), and in the distinct and complicated grooves on the carapace. A IV comes specially close to these two larvae, but has the fifth leg enlarged and much longer than 3 and 4, The paddles on legs 4 and 5 and enlarged propodus on 3 show a very strong resemblance.

Gurney (1937 *b*) is of the opinion that the differences exclude *Eretmocaris*

dolichops from the *Eretmocaris-Lysmata* group, and with it his A VII (here left out of the discussion), and suggests, as Coutière (1907) did previously for the genus *Eretmocaris* Bate, that it might belong to the Pandalidae. The presence in X of paddles on the three last legs brings the two species into a nearer relationship with the *Eretmocaris-Lysmata* group, and it seems that whatever family they represent there must be some affinity. The known larvae of the Pandalidae come very close in many ways to the Hippolytidae. The larvae of *Parapandalus richardii* have recently been described, and it has been suggested (Lebour, 1939) that figs. 45 and 46 of Gurney (1924) may belong to *Plesionika*, as they resemble in many ways those of *Parapandalus* but possess epipods. This is, however, by no means proved, and it may be that in *Plesionika* we have the adult of these *Eretmocaris* species. There is also the possibility that they may belong to *Nematocarcinus*, which comes between the Hoplophorids and Pandalids, and appears to be closely related to *Pandalus*. Kemp (1907 and 1910) has, however, suggested that larvae allied to *Caricyphus* may be the young of this genus. Another solution is that they may belong to still undescribed adults. The fauna of the deep waters of the Atlantic is by no means fully known, and new forms are continually being described. Especially do the various decapod larvae recently discovered show that there must be many more adults to be found, probably living in habitats difficult of access.

5. The Genus *Procletes* Bate. By Robert Gurney.

Bate's genus *Procletes*, which was founded as a member of the heterogeneous family Hectarthropidae, contained only one species, *P. biangulatus*, from the neighbourhood of the Aru Islands, though another was referred to as *P. ellioti* but not described.

Ortmann's *Atlantocaris gigas* has been referred to *Procletes* by Coutière and by Lenz and Strunck, but it is quite uncertain if *A. longirostris* Ortmann is really congeneric. Lenz and Strunck described a new species, *P. atlanticus*, but this is really a synonym of *A. gigas*. There are therefore only two species of larva belonging to the genus *Procletes*.

The *Discovery* material includes three specimens of *P. gigas*, and I have also two specimens of *P. biangulatus* from the Great Barrier Reef. As these larvae are of exceptional interest, and the structure of their appendages has not been adequately recorded, I give a redescription here.

Procletes biangulatus Bate. (Fig. 12, *a–h*.)

Bate. 1888. *Challenger* Report, p. 884, pl. 127. Aru Islands.
Lenz and Strunck. 1914. Südpolar Exp. p. 335. Straits of Macassar.

Great Barrier Reef, Station 50, Papuan Pass. Two specimens.

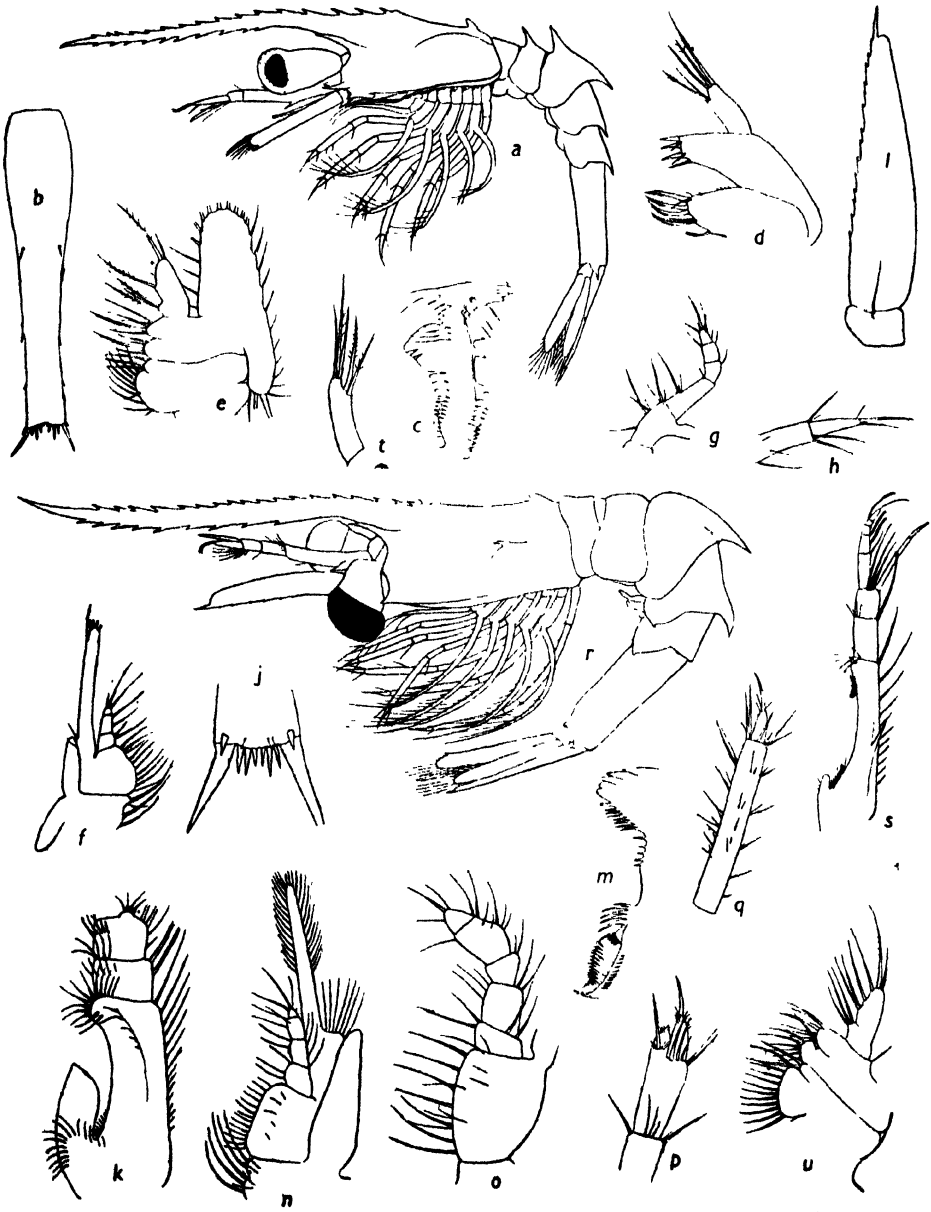

FIG. 12. *a–h. Procletes biangulatus*: *a*, *Procletes biangulatus*, 8·8 mm.; *b*, telson; *c*, mandible, about to moult; *d*, maxillule; *e*, maxilla; *f*, maxillipede 1; *g*, maxillipede 2; *h*, part of leg 1. *j–u. Procletes gigas*: *j*, end of telson; *k*, peduncle of antennule; *l*, antennal scale; *m*, mandible; *n*, maxillipede 1; *o*, maxillipede 2; *p*, end of leg 2; *q*, end of leg 1; *r–u*, specimen of 11·15 mm.; *s*, antennule; *t*, palp of maxillule; *u*, maxilla.

Length :	Rostrum	4	3
	Rest of body	7·25	5·8
	Total	11·25	8·8

(Smaller specimen.) Rostrum with sixteen dorsal teeth, of which three on carapace, and ten ventral. Carapace with very small dorsal papilla behind first dorsal spine, and large posterior papilla ; supraorbital and branchiostegal spines very large ; ventral margin with three strong teeth ; a small lateral ridge extends about half-way across the carapace from the posterior margin. Abdominal somite 1 with dorso-lateral process (not shown in figure) which, in the older specimen, overlaps the edge of the carapace. Somite 2 with forwardly directed dorsal spine ; somite 3 with dorsal ridge produced in front and behind into a strong spine ; somites 4 and 5 with posterior dorsal spine : pleura rounded, but somite 6 with pointed lateral process. Telson long and narrow, the greatest width about one-fifth the length, with three pairs of small lateral or dorsal spines : posterior margin with 6+6 spines, spine 2 large and divergent. Anal spine present.

Antennule with large ventral spine and rudiment of stylocerite ; flagella short. Endopod of antenna about two-thirds length of scale, which is narrow, with outer apical spine but no outer marginal spines.

Mandible without palp ; with three large movable spines on incisor part. Palp of maxillule unsegmented, with five setae. Maxilla, endopod unsegmented, with two small inner lobes ; lacinia well marked ; exopod very large in front, posterior lobe narrow, with one seta much larger than the rest.

Maxillipede 1, endopod of three segments, short ; epipod large, bilobed ; exopod with two outer basal setae. Maxillipede 2, endopod of four segments ; exopod with four setae only. Maxillipede 3, exopod with ten setae.

Legs 1–4 with long exopods ; legs 1 and 2 without trace of chelae. Pleopods absent ; uropods large, exopod with very small outer apical spine.

The larger specimen has the flagella of the antennule a little more developed and has small pleopods, but is otherwise the same.

PROCLETES GIGAS (Ortmann). Fig. 12, *j–u* ; Fig. 13, *a*.

Ortmann. 1893. Plankton Exp. p. 80, Taf. v.
Lenz and Strunck. 1914. Südpolar Exp. p. 334, Taf. XXII. Ascension. 3000 m. (*Procletes atlanticus*, sp. n.)

Discovery station 281. 00° 46′ S, 5° 49′ E., 850–950 m. 1 sp.
699. 12° 21′ N., 30° 07′ W., 370 m., 1 sp.
701. 14° 39′ N., 25° 51′ W., 242 m., 1 sp.

Specimen from station 281.

		mm.
Length :	Rostrum	14
	Rest of body	25·7
	Total	39·7

Rostrum with eighteen dorsal teeth, of which four are on the carapace; eleven ventral teeth. Carapace with small posterior papilla or spine and large supraorbital spine; there are three well-marked carinae, the two ventral ending in front in a large marginal spine; the dorsal carina ends in a large lateral spine, but is continued to the supraorbital spine as a less marked line. Ventral margin smooth.

Abdominal somites 2 and 3 with large posterior dorsal spines; pleura of somites 4 and 5 pointed; somite 6 rather short, with lateral pointed process.

Telson very long and narrow, with four pairs of dorsal spines and 4 + 4 terminal spines. Anal spine present.

Antennule, segment 1 with ventral spine and large stylocerite; segments 2 and 3 very short; flagella as long as peduncle, the outer flagellum swollen at base and slender distally, not distinctly segmented. Antennal scale narrowing distally, with large apical spine and a series of small teeth on outer margin; flagellum reaching beyond rostrum.

Mandible without palp, without large movable spines on incisor part. Maxillule, lacinia 1 rather pointed and turned inwards; endopod unsegmented, with six setae. Maxilla with lacinia 2 fairly well developed; endopod unsegmented.

Maxillipede 1 with large bilobed epipod; coxa large; endopod of four segments; exopod expanded at base, with many setae. Maxillipede 2, endopod very stout, of five segments; podobranch and epipod present. Maxillipede 3 with two arthrobranchs and a small epipod. Legs 1–4 with long exopods bearing many setae; leg 1 without trace of chela. Leg 2 with rudimentary chela. Small epipods present on legs 1–3, and an arthrobranch on legs 1–4.

Pleopods large, setose. Pleopod 2 endopod with appendix interna, but no appendix masculina.

Specimens from stations 699, 701.

		mm.	mm.
Length :	Rostrum	3·3	3·65
	Rest of body	7·5	7·5
	Total	10·8	11·15

Rostral teeth— $\frac{14}{7}$ $\frac{19}{9}$.

Carapace with large supraorbital and small pterygostomial spines ; posterior dorsal papilla large ; ventral margin smooth ; a conspicuous lateral spine present in the course of an ill-defined lateral carina. In one of the two specimens a ventral carina is faintly marked.

Abdominal somites 2 and 3 with large dorsal spines ; pleura of somites 3, 4 and 5 pointed ; somite 6 three times as long as deep, with lateral pointed process. Anal spine large. Telson with two pairs of lateral and 5+5 terminal spines, spines 2 and 4 the largest.

Antennule with large ventral spine and small stylocerite ; flagella small, unsegmented. Antenna, scale narrowing distally, with apical spine and outer marginal teeth ; flagellum broken. Mandible without palp. Maxillule, endopod unsegmented, with five setae. Maxilla with four well-marked inner lobes ; endopod unsegmented, with two small inner lobes ; exopod large, rather narrow proximally.

Maxillipede 1, exopod expanded at base and with six outer basal setae, six distal. Legs 1–4 with long exopods with 9–11 setae. No epipods nor arthrobranchs present. Legs 1 and 2 without trace of chelae. Pleopods present, small.

These two specimens agree so closely in their main characters with *P. gigas* that there can be little doubt they belong to that species ; but they are very much less developed in respect of the antennules and pleopods, and in the absence of well-defined carinae on the carapace. The much longer last abdominal somite is a larval feature.

Systematic position of *Procletes*.

Ortmann suggested that *Atlantocaris* might be the larva of an Acanthephyrid, but recognized that the absence of an exopod from leg 5 was not consistent with such an identification. Coutière (1907) regarded *Procletes* and *Atlantocaris* as very close to *Thalassocaris*, if not actually belonging to that genus. Lenz and Strunck accepted Coutière's suggestion as probable, but thought it possible that the larval species described may not all belong to *Thalassocaris*. "Vielleicht kommen auch noch andere Genera, wie z. B. *Acanthephyra*, in Betracht."

The two species, *P. biangulatus* and *A. gigas*, may be accepted as belonging to the same genus, or to two very closely allied genera ; but *A. longirostris* must be left out of consideration until it is better known.

The absence of an exopod from leg 5 is sufficient reason to make reference of these two larvae to Hoplophoridae impossible. This exopod is developed in such Hoplophorid larvae as are known, and there is no justification for believing that it could appear in the adult if absent in the larva. Reference to *Thalassocaris* has to meet the difficulty of the small size of the species of this genus, and the fact that they do not have carinae on the carapace. These carinae, which are so conspicuous in *P. gigas*, are not found in the younger stages, and are evidently adult rather than larval characters. According to

Kemp (1923) there are only two species of *Thalassocaris* certainly known, *T. lucida* (Dana) and *T. crinita* (Dana), which are very much alike and both small (about 20 mm.). As I have a specimen of the first post-larval stage of *T. lucida* I give below some description of it for comparison with *Procletes*.

If *Thalassocaris* is excluded the only other genus which can be considered is *Heterocarpus*, and I am convinced that these two larvae may be referred to that genus, and that *P. gigas* is actually the larva of *H. ensifer* A. Milne-Edwards.

In the first place this is a deep-water genus whose larvae may be expected in oceanic plankton, and the species may be large or very large. Within the genus the carapace may have as many as three lateral carinae, or one or more of them may be absent. In the majority of species there are two, and in *H. ensifer* alone are all three well developed, the dorsal ridge not extending across the whole length of the carapace.

Smith (1882, p. 63) described a species, *Pandalus carinatus*, of 48 mm. which is regarded by Faxon and others as a young form of *H. ensifer*, and in this specimen the dorsal ridge continues forwards to the orbit as a faint line, and has a lateral tooth standing at the anterior end of the ridge itself. The resemblance to *P. gigas* is exact, and the identity of the species can hardly be doubted. Smith's specimen has all the characters of the adult and has lost all trace of exopods, although it is much smaller than Ortmann's specimen of *P. gigas*. On the other hand, the size of the *Discovery* specimen is quite small enough to fit in with the *carinatus*-stage in which the lateral spine on the carapace is the only remaining larval character. It is probably not unusual among the larvae of the oceanic Caridea for larval life to be continued until the approach or onset of sexual maturity so that transformation, when it comes, is direct to the adult form, without intermediate post-larval stages. The evidence for such an assumption is the presence in some of the Caridean larvae in the *Discovery* material of an appendix masculina on pleopod 2. If this is so, the great size to which some of these larvae attain would present no difficulty unless it actually exceeded the maximum size of the presumed parent.

No suggestion can be made as to the exact position of *P. biangulatus*. In general form and structure of appendages it agrees closely with *P. gigas*, and it may provisionally be accepted as belonging to *Heterocarpus* also, but there are a number of differences—for example the form of the antennal scale—which make such an assumption rather uncertain. Specimens at a more advanced stage may provide better means of identification.

Some species, at all events, of *Heterocarpus* have small eggs, and consequently a series of normal larvae, but it has not been possible to find any younger larvae in the *Discovery* material to fit on to these older ones.

THALASSOCARIS DANAE Bate. Fig. 13, *b–h*.

Bate. 1888. *Challenger* Rep. p. 683.

Discovery station 1375. 34° 30′ S., 26° 19′ E. 210 m.

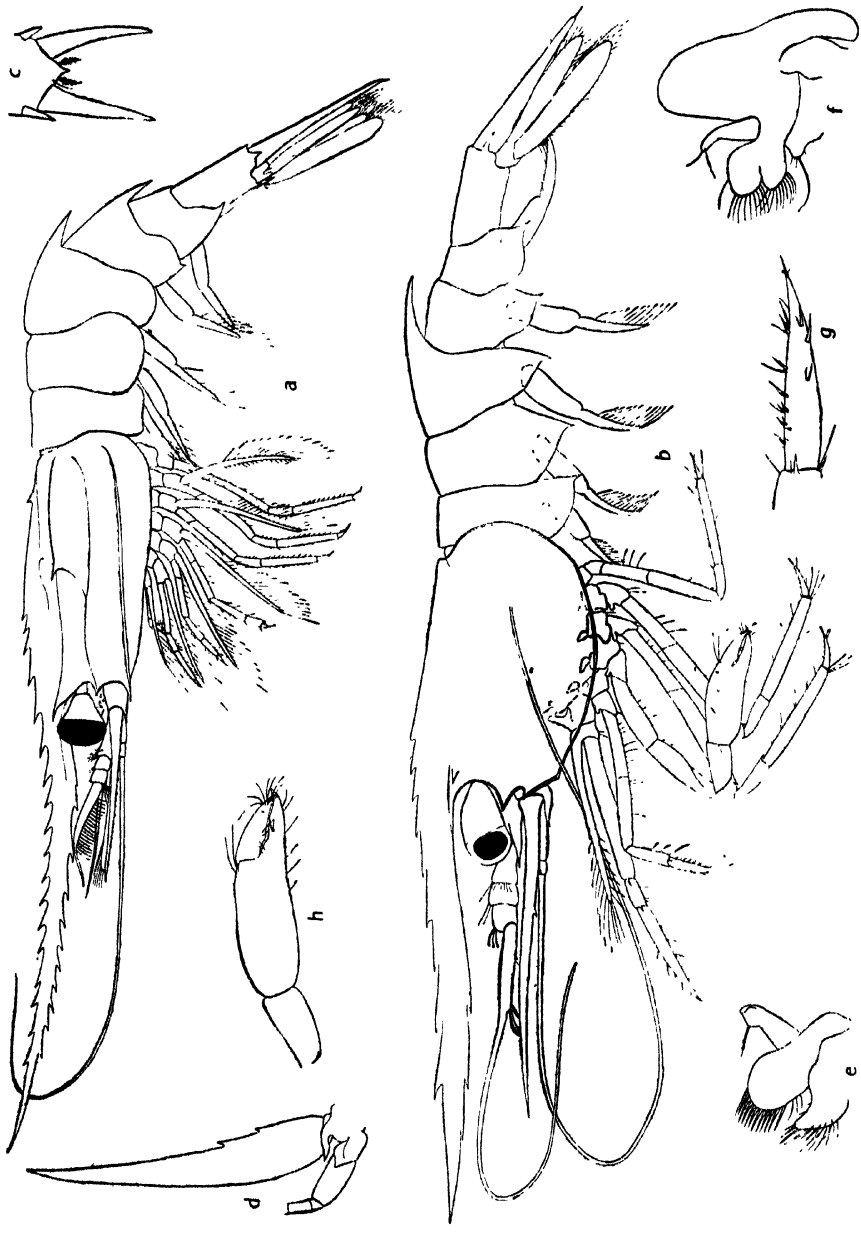

FIG. 13.—*a*. *Procletes gigas*, 39·7 mm. long. *b–h*. *Thalassocaris danae*: *b*, *Thalassocaris danae*, Station 1375; *c*, telson; *d*, antenna; *e*, maxillule; *f*, maxilla; *g*, end of leg 1; *h*, end of leg 2.

	mm.
Length : Rostrum	4·8
Rest of body	8·8
Total	13·6

Rostrum with eight dorsal and three ventral teeth. Carapace with small dorsal papilla behind the last dorsal spine and small supraorbital spine ; anterior margin with sharp projecting point below eye ; no branchiostegal nor pterygostomial spines.

Abdominal somite 3 with very large posterior dorsal spine ; pleura of somites 1–5 large, pointed ; somite 6 about twice as long as deep, with pointed posterior lateral process. Telson four times as long as wide, with two pairs of lateral spines ; apex pointed and bearing a pair of small feathered setae and two pairs of stout spines, of which the inner pair is very large.

Antennule with large pointed stylocerite, without otocyst ; outer flagellum very long, thickened at base. Antennal scale very long and tapering to a point, with two teeth on outer margin ; basis with stout curved spine.

Mandibular palp present, unsegmented, and without setae. Maxillule, proximal endite pointed, incurved. Maxilla, proximal endite small, with one very long seta ; distal endite bilobed. Maxillipede 1, basis not produced distally ; epipod large, bilobed. Maxillipede 2, propod flexed upon carpus, with dactyl articulated to its narrow end and not upon outer margin ; epipod large, with rudimentary podobranch. Maxillipede 3 with small arthrobranch and forked epipod ; exopod longer than ischiomerus. Legs 1–4 with vestigial exopods. Leg 1 without chela, the dactyl and propod fused. Leg 2 with large chela, the dactyl half length of palm, and palm twice as long as wide. Legs 3 and 4 with three inner spines on merus ; propod with five inner marginal spines, and one spine on outer margin. Leg 5 with four spines on merus and on propod. Very small epipods on legs 1–3 and an arthrobranch on legs 1–4, as in adult.

There can be no doubt that this is a young stage of *T. lucida* (Dana), presumably the first post-larval stage. Bate omits the supraorbital spine from his figure, and appears to have seen a long exopod on leg 1. This is probably an error, and his stage is the same as this one.

6. The larvae of some Palaemonidae from Bermuda.

By Robert Gurney and Marie V. Lebour.

Of the Palaemonidae of Bermuda the larvae of the following have been partially described :—

Anchistioides antiguensis.....	Stages 1 and 2.
Periclimenes americanus	Stages 1 and 5.
Brachycarpus biunguiculatus	Stage 1.
Leander tenuicornis	Stages 1 and 5 (?).

We are now able to give an account of the development from hatching to post-larva of *B. biunguiculatus*, and of the larva and post-larva of three species of Pontoniinae which can be identified with reasonable certainty as species of the subgenera of *Periclimenes*, *Periclimenaeus* and *Periclimenes* s. str. We have also stages 1 and 2 of a species of *Periclimenaeus*, the description of which by Mr. John Armstrong is in the press.

There are other forms taken in the plankton which cannot be identified, but which point to the presence at Bermuda of several species of Pontoniinae the adults of which have not yet been seen. It is remarkable that not one of the species of which we have obtained the post-larva can be assigned to a species already known there. In spite of the abundance of the adult *Anchistioides antiquensis* no larvae, in any stage, were taken either in the Reach or outside even when the adult was known to be breeding and larvae were actually hatched in the laboratory. The habitat of the adult still baffles investigation, and it appears that its larval history is equally mysterious.

Another species of which the larva should have been found is *Gnathophyllum americanum*. The habitat of the adult is unknown, but a few were taken at night in plankton in the Reach, though without eggs. In spite of its many peculiar characters the genus is probably allied to the Palaemonidae, and it seems possible that its larva may be of the bent and flattened type included in the *Mesocaris* group.

Our knowledge of the development of the Palaemonidae is now fairly extensive, particularly with regard to the Palaemoninae, but there are too many larval types which cannot at present be definitely identified. It has been shown (Gurney, 1938 *b*) that there is much variety of type within those larvae which are supposed to belong to the Palaemonidae, and it is particularly among the Pontoniinae that more examples are required of larvae of known parentage. The difficulty is great. Most of the Pontoniinae are tropical, commonly associated with coral reefs, and even when the first larva can be hatched no great advance is made unless it can be connected with later stages. All that we know with certainty of the later stages is the type belonging to *Periclimenes* subgenus *Ancylocaris*. Since the same type is found in two widely separated species, *P. calmani* and *P. americanus*, it may safely be assumed that this form, with legs 4 and 5 elongated, and the body not flattened nor bent will prove characteristic of all allied species.

The description given below of *Periclimenes longicaudatus* shows that the larva of *Ancylocaris* is far from being typical for the whole genus.

It is possible to make a rough division of the larvae which are supposed to belong to the Pontoniinae into two groups, the one which may be called the *Ancylocaris* group having the characters given above, and the other with legs 4 and 5, not, or but little, larger than leg 3, and the body doubly flexed at the junction of thorax and abdomen and at somite 3. This group may be called the *Mesocaris* group. It is probably best to define this group no more precisely

than this, since the definition already given (Gurney, 1936 *d*, p. 30) is evidently applicable to but few larvae, and we have no means for determining the relationship of those which do not fit it. It is certain that the group includes larvae of several genera. We describe below three larvae which can be proved to belong to species falling within the definition of the subgenus *Periclimenaeus*, so that we now know representatives of all three subgenera of *Periclimenes*. There remain, however, other larvae of the same group taken at Bermuda which cannot be assigned to a genus since they have not been followed to post-larval.

The grouping of the adult Pontoniinae presents much difficulty. The scheme given by Kemp (1922) is accepted as a great advance, and it no doubt approximates to a final solution ; but the proof of it depends upon whether new discoveries fit naturally into the scheme. This does not seem to be the case for the two Atlantic species *Coralliocaris atlantica* Rathbun, and *Periclimenes portoricensis* Schmitt, and there is some evidence (Gurney, 1938 *b*) that the true relationships of *Periclimenes diversipes* and *Harpilius gerlachei* are not correctly expressed by their present position. It is not certain that the three species referred to *Periclimenaeus* are really more closely related to *Periclimenes* than to *Coralliocaris* for example.

It seems likely that the larvae when known will greatly assist in the establishment of a final classification, but the process of identifying them is difficult and prolonged. In the meantime it may contribute to advance if those types which can be recognized as distinct can be described and figured, since at least it may be possible to frame a classification of the larvae which can eventually be compared with that of the adults.

The nomenclature of the spines on the carapace in both larvae and adult seems to require clarifying. Further consideration shows that the remarks on this subject by Gurney (1938 *b*, p. 3) do not correctly state the position.

In the adult the carapace bears, in addition to the supraorbital spine which may or may not be present, not more than two spines. It is commonly agreed that the spine which is generally present below the orbit is the antennal, and the other is called branchiostegal when it is at or near the anterior margin of the carapace, and hepatic when it is removed farther backwards, often to a line just behind and below the antennal. When there is a branchiostegal spine there is no hepatic, and vice versa. It is clear that the two spines are homologous, and differ only in position.

There is an apparent exception in the case of *Coutierea*. In this genus there is a very large antennal spine, and behind and above it is another spine which is ' postorbital ' rather than hepatic. There is also a tooth, or spine-like process, on the carapace margin which is regarded as pterygostomial. The interpretation of these three spines is most doubtful, but it would seem most probable that the ' pterygostomial ' is not a spine in the usual sense, but rather a notch in the margin without homology to a spine.

In the Hippolytidae there are again only two spines in addition to the supra-orbital, and the position of the ventral spine varies very much. In *Hippolysmata*, for instance, there is a ' branchiostegal ' at the anterior angle of the carapace, but in *Hippolyte ventricosus* it is removed backwards and higher up, while in *H. commensalis* it occupies the position of an hepatic spine, though it is called by Kemp (1925, p. 332) the branchiostegal.

In the larvae of the Palaemoninae the carapace may at first have an anterior point which has been called the pterygostomial spine. Later this point becomes a well-defined spine and moves upwards, while a second spine appears either below it (*Leander*) or behind it (*Brachycarpus*). We consider that the first spine to appear becomes eventually the antennal and the second either the branchiostegal or the hepatic spine. It is difficult to avoid ambiguity in descriptions, since it would seem odd to describe a spine in the pterygostomial position as antennal, though that is what it finally becomes.

While what has been said applies equally to the adult Pontoniid as to the Palaemonid, it is not so with the larva of the former. In *Mesocaris*, for example, there is a spine at the anterior angle of the carapace which corresponds to the pterygostomial of the Palaemoninae, but there is at the same time a spine above it which cannot be called anything but an antennal spine. In this case the antennal cannot derive from the pterygostomial. Either this early antennal is not the same as the adult antennal, or we must suppose that the pterygostomial has already moved upwards, and that the spine at the angle is really not pterygostomial, but the homologue of the branchiostegal-hepatic.

It is impossible to adopt a consistent nomenclature for the spines of the larva, and we are forced to refer to them by names which indicate their position at the moment rather than the names which describe their homology or final position.

Palaemoninae.

Brachycarpus biunguiculatus (Lucas). (Figs. 14, 15.)

Stage 1 of this species has already been described (Gurney, 1938 *b*, p. 8) from specimens hatched in the Bermuda Biological Station, and all the later stages have now been obtained from the plankton, proving that the larval species *Retrocaris spinosa* Ortmann (Palaemonid D.I., Gurney) is the final larva of *Brachycarpus*. The complete proof was afforded by the moulting of the larva into a post-larva which could be identified as *B. biunguiculatus*.

Stage 1 was again obtained by hatching in the laboratory, and a few larvae moulted to stage 2. Of the succeeding stages, taken in plankton, there are not many specimens. The differences both in size and structure between the stages which follow stage 3 are very small, and it may be that all of them are not necessarily passed through by each individual. In two cases only was the succession of stages proved by moult,

Stage 1. The abdomen is colourless except for a small red chromatophore in somite 3, but the thorax is bright red in the gastric region, and there are red chromatophores in and above the eye.

The structure has already been described.

Stage 2. Length 2·37 mm. (Fig. 14 *a*.)

The carapace has one median tooth at the base of the rostrum and a large supraorbital spine; the anterior angle is sharply pointed. The abdomen is unchanged except that there is a minute posterior tooth on the pleura of somite 5. The telson has 8+8 spines, the middle pair very minute. The antennule has a peduncle of two segments. The antenna is unchanged. The appendages are the same, except that legs 1 and 2 are developed. The exopods have six setae, but the posterior seta of the proximal pair is very small and may even be absent.

Stage 3. Length 2·75 mm. Fig. 14 *b*.

The carapace has two dorsal teeth. Abdominal somite 3 has a procurved dorsal spine, and the lateral spines of somite 5 are larger. The telson is separated from somite 6 and has 8+8 spines, of which one is on the outer margin. The endopod of the antennule appears as a small bud. The antennal scale is constricted at the end beyond the single outer seta, and has traces of three distal segments; the endopod is a straight rod nearly equal to the scale, with the basal segment separated, and four small distal setae. Legs 1 and 2 are developed as in stage 2, and there are rudiments of legs 3 and 4. The uropods are developed, the branches not jointed, and the endopod without setae.

As in stages 1 and 2 the colour is almost confined to the gastric region.

With this stage the 'Retrocaris' form is first assumed. This stage has already been figured from the neighbourhood of Rio de Janeiro (Gurney, 1924 *c*, p. 126).

Stage 4. Length 3 mm. (Fig. 14, *c–g*.)

The rostrum is longer than the eyes and has one basal tooth. There are two dorsal teeth on the carapace, a large supraorbital and a pterygostomial spine. The telson is widest at the end, its length 2·2 times its greatest width; spines 1 and 2 are on the outer margin near the end. There is no anal spine. The antennal scale is fully formed, and unsegmented; the endopod is a little longer than the scale, with two long distal segments and three short proximal segments, of which the first is actually a part of the basis; the basis has no spine.

The maxillule is unchanged. The maxilla is the same, but the exopod has nine setae, and the proximal lobe of it is not produced and bears one apical seta.

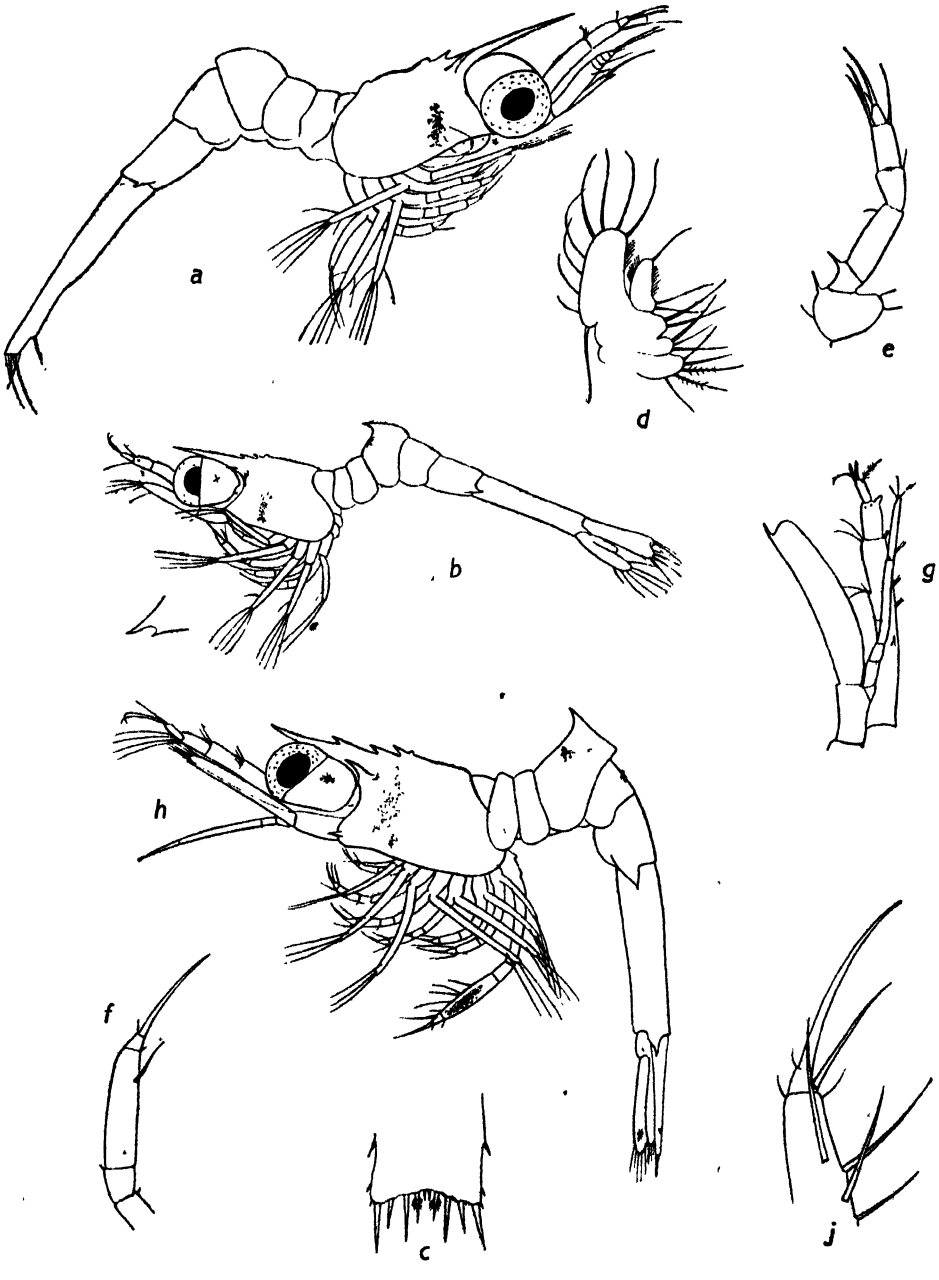

FIG. 14.—*Brachycarpus biunguiculatus*. *a*, Stage 2; *b*, Stage 3; *c–g*, Stage 4; *c*, telson; *d*, maxilla; *e*, leg 2; *f*, leg 5; *g*, antenna and antennule; *h*, Stage 5; *j*, Stage 5, leg 5.

Maxillipede 1 has an endopod of three segments, the basis large, not produced, and with few setae. Maxillipede 2 has a single small seta on the basis, and short, stout, endopod of three segments.

Legs 1–5 are developed, leg 4 with exopod with six setae. Legs 1–4 are alike, legs 1 and 2 without trace of chelae ; the basis and ischium each have a strong inner spine. Leg 5 is much larger than the others, without posterior spine on the basis. The propod has one strong inner seta, and the dactyl is small, with a single terminal spine and a small outer seta. There are no pleopods.

Stage 5. Length 3·62 mm., moulted from stage 4. (Fig. 14, *h–j*.)

The carapace and rostrum are as in stage 4. The telson is unchanged, though a trifle narrower. There is a very small anal spine.

The antenna is the same, but the flagellum is longer. Leg 5 is very large, the propod with four strong spines and strongly pigmented with orange-red. The dactyl has a long inner spine. The coxa has a posterior spine, but the ischiomerus has no spines. There are no gills and no pleopods.

At this moult there is very little change, but leg 5 has assumed the form and arming characteristic of the fully formed *Retrocaris* larva, and makes it possible to link up the latter with the early stages with certainty.

A larva of a similar stage, but larger (5–6 mm.), from South Georgia has been described by Coutière (1907 *a*) as *Retrocaris antarcticus*. This larva lacks the lateral spines on somite 5 and cannot therefore be referred without doubt to *B. biunguiculatus*.

Stage 6. Moulted skin only. (Fig. 15, *a–c*.)

The pterygostomial spine has now moved a little upwards towards its final position as the antennal spine, and the hepatic spine has appeared behind it, but the carapace and rostrum are otherwise the same. The abdominal pleura 1–5 are rounded. The telson is five times as long as wide, with greatest width in front. It has two pairs of lateral and 6+6 terminal spines.

Segment 1 of the antennule has a small ventral spine and rudiment of the stylocerite ; the endopod is slender and unsegmented. The basis of the antenna has a spine, and the flagellum is twice as long as the scale (2 mm. long), segmented throughout.

The exopod of the maxilla is large, fringed with setae. The maxillipedes and legs 1–4 are unchanged. Leg 5 has a row of spines on the outer margin of the ischiomerus, and one spine on the carpus. The uropods are large, with numerous setae, the endopod having a number of sensory setae on the dorsal surface.

Stage 7. Moulted from stage 6. Length 6·4 mm. (Fig. 15, *d*.)

Carapace as before, but the rostrum has a small unserrated tooth midway between the end and the first large serrated tooth. The pleura of somites 1 and 2

have small points, that of somite 3 being rounded or with very minute posterior point. The dorsal spine of somite 3 is long and sharply pointed. The telson is unchanged.

The flagellum of the antenna is differentiated into a peduncle of three short diagonally jointed segments and one long one, and a flagellum of 2·3 mm. Legs 1 and 2 are not chelate. Leg 5 has a large coxal spine, and two spines on the carpus.

A small rudiment of a pleopod was seen on somite 2 only in this single specimen.

Stage 8. Length 7·8 mm. (Fig. 15, *e*.)

The rostrum has one large and three small dorsal teeth, and one small ventral tooth. The telson is unchanged, except that the posterior margin is more convex.

Maxillipede 1 has a basal expansion of the exopod with six setae. Legs 1 and 2 have no chelae. Very small pleopods are traceable on somites 1–4.

This stage has already been figured (Gurney, 1938 *b*, figs. 50–52).

Stage 9. Length 9·7 mm. (Fig. 15, *f*, *g*.)

The rostrum has five dorsal teeth, nearly equal, and two ventral teeth. The exopod of the antennule has a first rudiment of the accessory flagellum, and legs 1 and 2 have rudimentary chelae. The pleopods are larger, with small rudiments of endopods, and setae on the exopods of 1–4, the largest being 1 and 2.

Stage 10. Length 11·8 mm.

The antennule is the same. The chelae of legs 1 and 2 are more developed, and the pleopods are larger, pleopod 5 being now jointed and with setose exopod.

Stage 11. Length 15·8 mm.

This is the last larval stage, which has already been described (Gurney, 1938 *b*, figs. 39–49).

A specimen of this stage was taken on 11 July 1938, and moulted to post-larval on 16 July. It was not measured or closely examined when alive, but appeared to be colourless. The cast skin showed all the characters of the form already described. The only additional point to be noted is that the dorsal margin of abdominal somite 1 is minutely crenulated, as is also the posterior dorsal margin of somite 5.

Post-larval stage 1. Length 18 mm. (Fig 15, *h–m*.)

The animal was quite colourless except for the large, intensely black, eyes.

The rostrum is straight, extending nearly to the end of the antennal scale,

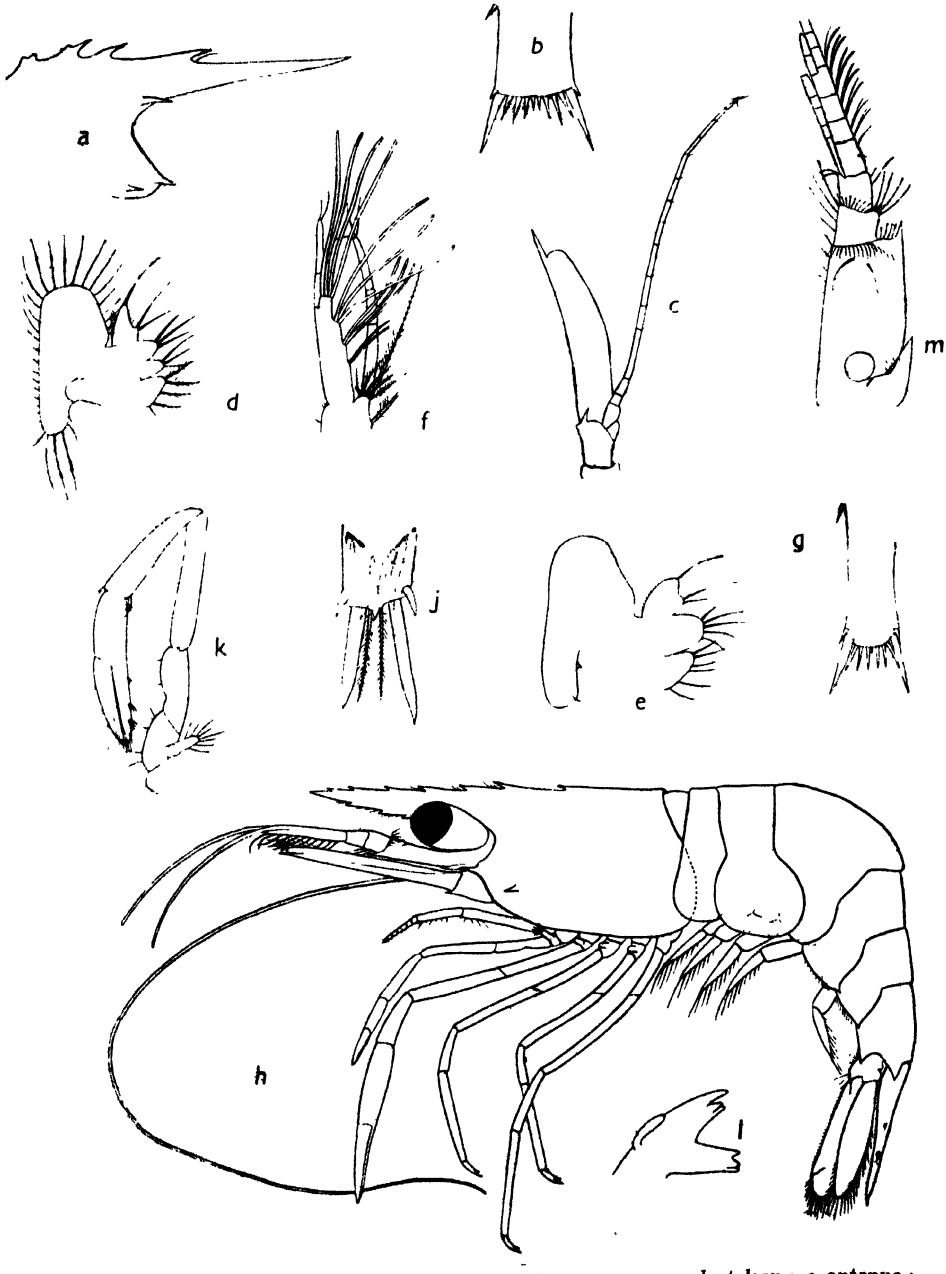

FIG. 15. *Brachycarpus biunguiculatus*. *a–c*, Stage 6. *a*, carapace; *b*, telson; *c*, antenna; *d*, Stage 7, maxilla; *e*. Stage 8, maxilla (setae of exopod omitted); *f*, *g*, Stage 9. *f*, antennule; *g*, telson; *h–m*, post-larval; *h*, post-larval stage 1; *j*, telson; *k*, leg 1; *l*, mandible; *m*, antennule.

with three ventral and five dorsal teeth. The carapace has two dorsal teeth and hepatic and antennal spines.

Abdominal somite 3 has a dorsal ridge which is the vestige of the larval crest. The pleura of somites 4 and 5 are pointed. The telson has two pairs of lateral spines, a small apical point, and two pairs of apical spines together with three pairs of feathered setae. It appears that all but one of the larval spines are represented.

The antennule is fully formed, with stylocerite and statocyst, but the free sensory part of the outer flagellum is very short, and of two segments only, the basal part having four segments. In an adult female from Bermuda there are eighteen segments in the basal part, and the free sensory flagellum is nearly as long as the basal part.

The mandible has a small unsegmented palp. The mouth-parts are as in the adult. Maxillipede 2 has a small rudiment of a podobranch. Maxillipede 3 has an epipod and two small arthrobranchs.

Legs 1–4 retain vestiges of the exopods, that of leg 1 with setae. In leg 2 the fingers of the chela are straight, with simple smooth edging membrane. In an adult female the fingers are curved, with a similar membrane There are, in this adult specimen, four very indistinct protuberances near the base of the dactyl, and two on the fixed finger, but these can hardly be described as ' well developed teeth ' such as Kemp found (1925, p. 313). Legs 1–3 have the dactyl bifurcate as in the adult. The sex cannot be determined, but there is no appendix masculina on pleopod 2.

The following measurements show the changes which take place in legs 1 and 2 :—

	Leg 1.			Leg 2.		
	dact.	palm.	carpus.	dact.	palm.	carpus.
Last larva	100	53	74	100	78	52
Post-larval 1	100	86	168	100	107	72
Adult female	100	100	233	100	114	71

The proportion of dactyl to palm and carpus is very much greater in the larva than in the adult, as it is in *Palaemonetes varians* (Gurney, 1924 *a*, p. 323) and *Leander longirostris* (Gurney, 1924 *b*, p. 973), but the difference is by no means so great in *Brachycarpus* as it is in the other species, and in the first post-larval stage the proportions of the adult are already established in leg 2, whereas they are not reached until near maturity in *P. varians*. The excessive size of the dactyl in the last larva is somewhat remarkable, since it is quite short, as in the other legs, before the chela is formed. The transitional stage of the last larva cannot be regarded as a larval character at all, and it might be suggested that we see here a case of recapitulation pointing to an ancestral form in which the legs were more heavily built, and with much longer dactyls, than those of present day Palaemonids. The relative shortness of the carpus in leg 2 of the adult is a case of the retention of a larval character.

Remarks.—This series of stages is of rather special interest in that it leads up to one of those large larvae of the high seas which Coutière believed to be abnormal. There is evidently a long period of larval life, and it is possible that the number of stages is really indefinite. In European species of *Leander*, e.g., *L. serratus*, which as adults grow fully as large as *B. biunguiculatus*, the last larva measures 8–10 mm. at most, and the post-larva very little more, so that the last larva and post-larva of *B. biunguiculatus* are nearly double the size. The fact that one of these very large larvae has been proved to transform to a perfectly normal post-larval stage does not exclude the possibility that this transformation may take place also at smaller sizes, since the larva is almost fully formed at about 8 mm. The prolonged larval life may explain the wide distribution of the adult, from the Mediterranean to the West Indies and, possibly, the Red Sea. The larva has been taken as far south as 24° 40′ S., and even near South Georgia, if *Retrocaris antarcticus* belongs to this species, and the adult will no doubt be found to extend farther south than present records show. It is, in Bermuda, a nocturnal littoral species which can easily escape notice ; indeed, since its capture by the *Challenger* expedition it was not seen at Bermuda again until 1936, when it was found to be common in certain places.

The identity of *R. contraria* Ortmann remains uncertain. It was recorded by Ortmann from the Brazilian coast, and specimens have been taken by the *Discovery* in much the same region, so that it may be expected to belong to a South American species of *Palaemon* or to an unknown species of *Brachycarpus*.

Menon (1938) has recently described the first two stages of *Palaemon rudis* and *P. lar* from Madras. These are almost indistinguishable from similar stages of *Brachycarpus*, and prove that a normal series of free-swimming larvae may be found in the genus *Palaemon*. The later form of the larvae is unknown.

LEANDER TENUICORNIS (Say).

Palaemon tenuicornis Say, Proc. Acad. Sci. Philadelphia, 1. p. 249, 1818.

Stage 1 and a later stage, presumed to be stage 5, have been described (Gurney, 1938 *b*, p. 4, and 1939), and some of the peculiarities of the species, as compared with other Palaemoninae, have been pointed out. Three specimens have now been seen which seem to represent the penultimate stage, with all the legs and small pleopods developed. There is almost certainly another stage between this and stage 5, so that there must be at least eight stages in all.

At this stage the larva seems to be identical with ' Palaemonid B.R. IX ' (Gurney, 1938 *b*, p. 39) which has been described as a member of a ' Cryptoleander ' group. These larvae agree in the following characters :—

(1) Leg 5 is very greatly elongated, precociously developed, and has long spines at the end of the propod, and a spine at the base of the dactyl.

(2) Leg 4 has no exopod.
(3) The endopod of the maxilla has no basal lobe.
(4) The basis of maxillipede 1 is more or less hatchet-shaped.

In the general form of the body and the dorsal spines they agree with other Palaemoninae.

LEANDER AFFINIS H. M.-Edw.

This is a common littoral species in Bermuda, and the larvae were hatched in the laboratory on 19 June 1938, and moulted three days later to stage 2. These larvae are practically identical with those of typical *Leander* such as *L. squilla*, but can be distinguished from all species by the large size of the pair of dorsolateral spines on somite 5. In *L. squilla* there is a pair of spines on this somite, but they are small.

The general colour in stage 1 is pink, the telson colourless. In stage 2 there in profuse orange-red in thorax and abdomen up to somite 3. Somite 6 and telson are colourless.

PONTONIINAE.

PERICLIMENES (s.g. *Periclimenes*) LONGICAUDATUS (Stimpson) ?

Urocaris longicaudata Stimpson, 1860, Proc. Acad. Sci. Philadelphia, p. 39.

No larva is so far known which undoubtedly belongs to *Periclimenes*, subgenus *Periclimenes*, although several larvae have been described which belong to the subgenus *Ancylocaris* (Gurney, 1936 *d*, 1938 *b*). A single larva in the last stage was obtained from plankton from just outside Bermuda (outside Gurnet Rocks, 20 fathoms, 5. 5. 39). This was kept alive in a bowl, and changed to a post-larva in the laboratory. Further changes resulted in three further stages, the third young stage then being killed. Thus a series of five stages was obtained.

The young forms belonged to a species of *Periclimenes*, subgenus *Periclimenes*. The latest one (third young stage) was sent to Dr. Fenner Chace, jr., who kindly identified it as probably, but not certainly, belonging to *Periclimenes* (*Periclimenes*) *longicaudatus* (Stimpson). It differs from this species in the rostrum, which has fewer teeth, and in having the third abdominal segment produced into a hood in a similar way to *Periclimenes* (*Periclimenes*) *aesopius* (Bate), redescribed by Kemp (1922). The small number of teeth in the rostrum may be due to its youth, but it is remarkable that there are no more teeth in the third young stage than there are in the second. With regard to the third abdominal segment, this is unlike the larva in form, and is a serious difference from *P. longicaudatus*. On the other hand, it has no antennal spine which is characteristic of that species. It is therefore regarded as belonging to *P. longicaudatus* with a query.

It is interesting to find that the larva does not agree with those known which belong to the subgenus *Ancylocaris*, but have much closer relationships with the *Mesocaris* groups. Gurney (1938 *b*) summarises the characters of the larvae of the subgenus *Ancylocaris* and of the *Mesocaris* group so far known. In the latter he has placed several different forms which may not be very closely related, but have certain features in common—they have an acute double flexure of the depressed body and abdomen, legs 3–5 are of about the same length, and there is no basal lobe on the endopod of the maxilla. The present larva agrees in these three characters, but differs in many ways from the larval genus *Mesocaris* as defined by Gurney. Thus it has a very short rostrum with one tooth only ; the telson has nine terminal spines ; legs 3–5 are without exopods. It agrees, however, with *Mesocaris* in having a ventral spine on the antennule, in the maxillule and maxilla, and in the general form of the legs. In having a central spine on the hind margin of the telson, the unique specimen of the last larva may possibly be abnormal as it disappears in the post-larva. The description and figures are taken from the cast skin.

Last larval stage ca. 5 mm. long. (Fig. 16, *a*, *b*.) When living the body was much bent with a double flexure, the whole being depressed. It was very transparent with red chromatophores scattered on the body—antennules, antenna, eye stalks, legs, on the second, third, and sixth abdominal segment, and on the telson. Captured on 5 May, it changed to the post-larva on 11 May, the post-larva to first young stage 15 May, the first young to second young stage 24 May, and the second to the third young stage on 31 May.

The last larva has a short rostrum with one tooth, small supraorbital spines, antennal (?) spine and pterygostomial point. The region of the green gland at the base of the antenna is much produced. The antennule has a large ventral spine on the proximal segment. The eyes have very long stalks. The abdominal segments are rounded and the third slightly elongated and oblique, but not produced into a true hump or tooth. The sixth segment is very long, as long as segments 3–5 together. The telson has one pair of lateral spines and nine terminal spines. It is long and narrow, and almost parallel-sided. The mandible has only a few teeth on the cutting part and is very narrow. The maxillule has an unsegmented endopod with two terminal setae and two well-developed lobes, the inner lobe being pointed, and bearing an outer hair. The maxilla has a very small endopod, with one terminal seta and no basal lobe, and three very much reduced lobes bearing two, two, one setae. The exite is large and bears six setae anteriorly and two posteriorly, the lower outer margin having no setae. The second maxillipede has a broad base with one inner seta, a long exopod with four setae, and a strong endopod with four segments, the dactyl ending in a strong hook. The propod of the third maxillipede has two strong hooks at its junction with the dactyl, which is composed of a long simple hook with setae. Its exopod bears six setae. The first and second legs are chelate, with a long narrow dactyl and very much swollen propod ; the exopods bear six setae. Legs 3, 4, and 5 end in long simple dactyls,

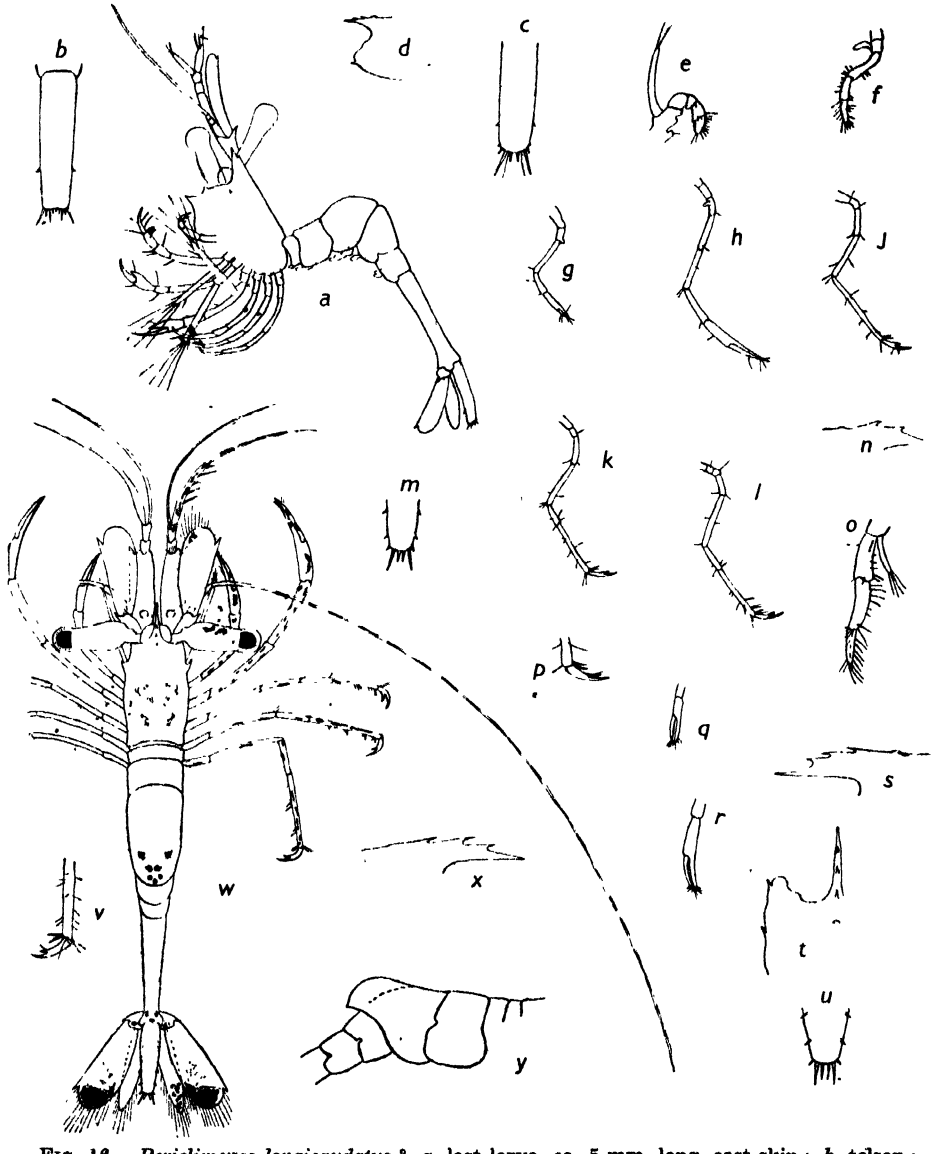

FIG. 16.—*Periclimenes longicaudatus* ? *a*, last larva, ca. 5 mm. long, cast skin; *b*, telson; *c–l*, post-larva from last larva cast skin; *c*, telson; *d*, rostrum and anterior part of carapace; *e*, second maxillipede; *f*, third maxillipede; *g*, first leg; *h*, second leg; *j*, third leg; *k*, fourth leg; *l*, fifth leg; *m–r*, first young stage from post-larva cast skin; *m*, telson; *n*, rostrum; *o*, third maxillipede; *p*, end of third leg; *q*, end of first leg; *r*, end of second leg; *s–v*, second young stage from first cast skin; *s*, rostrum; *t*, rostrum and carapace, dorsal; *u*, telson; *v*, end of fourth leg; *w–y*, third young stage from second 6·5 mm. long; *w*, third young stage; *x*, rostrum *y*, abdomen.

3 and 4 having two hooks at the junction of propod and dactyl, and there is a tooth at the outer margin about half way along the merus. Leg 5 has a simple dactyl without hooks at the base.

The post-larva from last larva. (Fig. 16, *c–l.*) Length ca. 4·5 mm. The descriptions of this stage and those of the first and second young stages are from the cast skin. The rostrum has two teeth in front of the dorsal organ ; the supraorbital spine has disappeared, but the antennal remains. The hepatic was not seen, but this is present in the second young stage. The mandible has distinct cutting and molar parts. The maxilla has no setae on the third lobe, which is very much reduced. The antennule has a round otolith, a short lateral process, and a wide proximal peduncular segment with an external hook. The telson is slightly rounded, with four spines and two long hairs between the third and fourth, the central tooth having disappeared. The second maxillipede has two setae on the exopod, and a broad endopod of four segments. The third maxillipede has a reduced non-setose exopod and a three-segmented endopod. The first leg is short and has small simple chelae, the second leg has also a small vestige of an exopod, but is much longer than the second, with long simple chelae. Legs 3 to 5 are biunguiculate, with a pair of stout teeth at the end of the propodus. This stage is now recognisable as belonging to the subgenus *Periclimenes* of the genus *Periclimenes*. This changed to the first young stage.

The first young stage from the post-larva. (Fig. 16, *m–z*) Length ca. 5·5 mm. The rostrum is like the post-larva. The exopod of the third maxillipede has four setae. The chelae of the first leg are long, but smaller than the second. The telson has two pairs of lateral setae and six terminal spines.

The second young stage from the first. (Fig. 16, *s–v.*) Length ca. 6 mm. There are three dorsal teeth on the rostrum. There is an hepatic spine and also an antennal (or branchiostegal ?). The mandible is deeply cleft. The telson is as in the previous stage.

The third young stage from the second. (Fig. 16, *w–y.*) Length 6·5 mm. There are still three teeth on the rostrum. The eye-stalks are long. There is a peculiar tooth-like prominence on the third abdominal segment. The antennal scale is very broad. There is no antennal spine, but the hepatic spine is conspicuous. The telson is as in the last stage.

Whether or no this species is correctly named it certainly is very close to *Periclimenes* (*Periclimenes*) *longicaudatus*, and shows that the type of larva in that subgenus is quite unlike that of the subgenus *Ancylocaris*. The larva

is not unlike Gurney's Palaemonid R.S. III (figs. 139–145), and this may possibly belong to the same subgenus.

PERICLIMENES, subgenus PERICLIMENAEUS.

The three species described under this heading are placed in the subgenus *Periclimenaeus* on the advice of Dr. Fenner Chace jr. They are apparently closely related to *Coralliocaris*, but lack the large protuberance on the dactyls of legs 3–5, and there is no hepatic spine.

PERICLIMENES (PERICLIMENAEUS) WILSONI (Hay) ? (Fig. 17, *a–q*.)

Coralliocaris wilsoni Hay (Bull. U.S. Bur. Fish. vol. xxxv. 1918, p. 393).

Last larval stage (fig. 17, *a–g*). Length 4·3, 4·7 mm.

The body is broad, rather flattened, and sharply flexed at thorax and somite 3 ; somite 6 is laterally compressed. The rostrum is shorter than the eye, with dorsal crest bearing two teeth. The carapace has a very minute supraorbital spine, an antennal spine and its anterior angle pointed. The telson is four times as long as wide, with one lateral spine situated a little beyond the middle ; at the end there are six stout spines, of which the outer pair are the longest and the second the shortest. In one of the two specimens there is also a pair of very small spines in the middle. The antennule has a small ventral spine and rudimentary stylocerite on segment 1 ; the outer flagellum is not cleft. The antennal scale is a little more than three times as long as wide, with small apical spine. The flagellum is about twice as long as the scale, and there is a very small ventral spine on the basis.

The mandible has a three-toothed incisor process and five or six movable spines between it and the small molar portion. The endopod of the maxillule has two very small setae. The exopod of the maxilla is fringed with hairs and not setae on its outer margin, and the endopod is simple, without basal lobe, and with one apical seta. The endopod of the first maxillipede has three segments and three apical setae ; the basis is not protuberant. Maxillipede 2 has a spine and a seta on the basis, and the terminal claw conspicuously fringed. Maxillipede 3 has no large spine on the ischiomerus.

Legs 1 and 2 are chelate, leg 2 very much the larger. The chela of leg 2 is as long as ischiomerus and carpus together, and the palm rather more than one and a half times as long as wide. Legs 4 and 5 are equal and alike, except that leg 4 has three spines at the end of the propod and leg 5 has only one ; the spine at the end of the dactyl of leg 5 is simple. Legs 1–4 have exopods.

Colour.—Rich red in thorax, in the basal parts of the anterior appendages, and particularly in the middle parts of legs 4 and 5. Somite 3 is very red, but somite 6 and the tail fan are colourless.

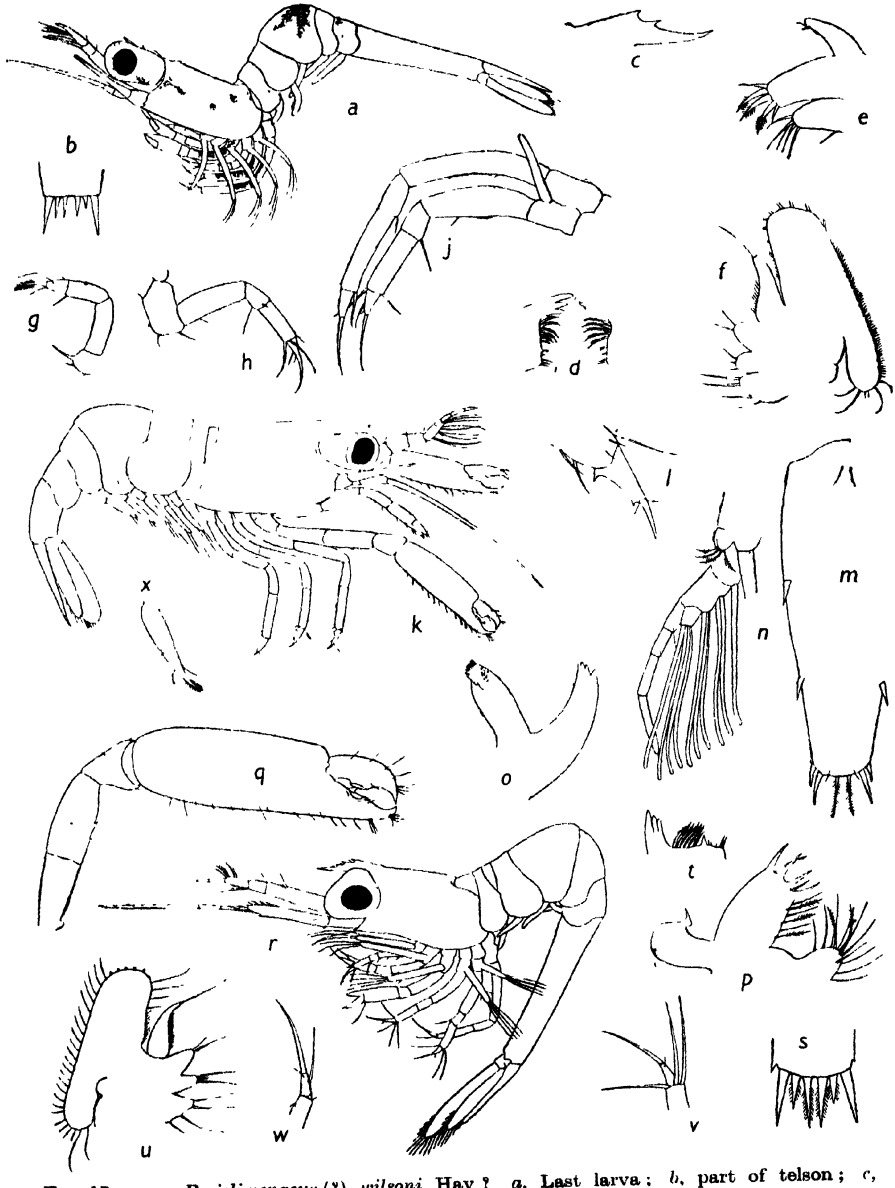

FIG. 17.—*a–q. Periclimenaeus* (?) *wilsoni* Hay ? *a*, Last larva; *b*, part of telson; *c*, rostrum; *d*, mandibles; *e*, maxillule; *f*, maxilla; *g*, maxillipede 2; *h*, maxillipede 3; *j*, legs 4 and 5; *k*, post-larval 1; *l*, dactyl of leg 3; *m*, telson; *n*, part of antennule; *o*, mandible; *p*, maxillule; *q*, leg 2. *r–x. Periclimenaeus* (?) B: *r*, last larva; *s*, part of telson; *t*, mandible; *u*, maxilla; *v*, end of leg 4; *w*, end of leg 5; *x*, end of maxillipede 2.

Three specimens of this form were taken. One of them moulted to post-larval, but the moulted skin was almost entirely devoured by the post-larva. As the specimen could not be closely examined in life it is not absolutely certain that it was identical with the form described above ; but the colour was the same, and such appendages as survived (e.g., maxilla) agree exactly. No other larva with this conspicuous colouring was seen.

Post-larval 1. (Fig. 17, *k–q*.) Length 5 mm.

The body is stout and rather depressed. The rostrum is longer than the eyes, with three dorsal teeth. The carapace has only a small antennal point and no hepatic spine. The telson is about three times as long as wide, with two pairs of lateral spines and two pairs of apical spines, with a pair of feathered setae between them.

The basal segment of the antennule has a small spine at its outer distal angle, and a small stylocerite which does not cover the statocyst. The outer flagellum has two thick basal segments and four slender distal segments ; the accessory flagellum consists of a single small segment bearing aesthetes.

The mandible has no palp ; molar and incisor parts are about equal, and the former has three very small teeth ; the molar part has a brush of small spinules and no large teeth. The endopod of the maxillule is small and bears a single inner curved process. The maxilla has a large exopod which is not very wide ; the endopod is unsegmented, simple, without basal lobe. The basis of maxillipede 1 is rather prominent, and the endopod unsegmented.

Leg 1 is slender, the chela longer than the carpus, and the dactyl a little shorter than the palm. Leg 2 on the right side is larger than on the left. The right chela has the palm parallel-sided, two and a half times as long as wide, and two and a half times as long as the dactyl. The dactyl is curved, with an inner protuberance, the face of which is hollowed ; the fixed finger has a hollow corresponding to the process of the dactyl, and a blunt process which seems to serve as a guide for the engagement of the one with the other. The left leg is simpler, the dactyl having a small roughened area corresponding to the process of the right leg, and a corresponding roughened papilla on the fixed finger. Leg 3 is a little longer than legs 4 and 5, and each has a similar dactyl with two small teeth, one at the base and one at the base of the distal claw. Legs 1–4 have vestiges of the exopods.

Colour.—The animal appeared to be colourless, but, under the microscope showed a number of minute dark chromosomes all over the body. All trace of the bright red of the larva was lost.

Remarks.—It is probable that considerable changes in structure would take place with growth since the individual is far from having attained the adult form of antennule and gills, so that identification is difficult. I am much indebted

to Dr. F. A. Chace for examining the specimen. While naturally unable to give any positive identification, he points out its resemblance to *Coralliocaris wilsoni* Hay *. The resemblance is indeed very close, particularly in the structure of the right chela, though there is not the great disproportion in size between right and left sides which Hay describes. There is also great difference in the rostrum which, in *C. wilsoni*, has 11–13 dorsal teeth, but both these differences may well be expected to disappear with growth. The last three legs are said to have a ' short conical dactylus ', which cannot be said of the Bermuda species. It seems best, however, to refer it provisionally to Hay's species, but it cannot be included in *Coralliocaris* as at present defined. The only genus in which it can be included is, as Dr. Chace points out, *Periclimenes*, subgenus *Periclimenaeus*.

It cannot belong to the species of *Periclimenaeus* of which the first and second larval stages are described below, since the differences in the form of the large chela are too great to be accounted for by age, and the form of the telson is very different. The large spine on the ischiomerus of the third maxillipede in the larva is a character which is not likely to be lost in later stages.

PERICLIMENES (PERICLIMENAEUS) Sp. B. (Fig. 17, *r–x*.)

Last larva. Length 5·65 mm.

The body is broad, rather depressed, and much bent at somite 3. The rostrum is shorter than the eye and bears three dorsal teeth. The carapace has a very minute supraorbital spine, and an antennal spine exactly the same as in *P. wilsoni*. The telson is four times as long as wide, with two pairs of lateral spines. There are usually six terminal spines, of which the second pair are the shortest, but in one specimen there is also an outer pair of very small spines (fig. 17, *s*). The antennule has a small stylocerite, and there are two slender segments beyond the thickened basal part of the outer flagellum. The antennal flagellum is about three times as long as the scale, and there is a small spine on the basis.

The mouth-parts do not differ from those of *P. wilsoni*, except that the exopod of the maxilla is fringed with setae throughout. The chela of leg 1 is slender. the palm more than twice as long as wide, and the dactyl about two-thirds as long as the palm. The chela of leg 2 is very large, the width of the palm more than half the length, and the dactyl half the length of the palm. Legs 4 and 5 are equal, and leg 5 has a simple spine on the dactyl, and one spine only on the propod. There are exopods on legs 1–4.

Colour.—The whole body is pink, the legs colourless.

We have three specimens of this larva in the last stage, and two in an earlier stage with legs 4 and 5 rudimentary. The specimen from which the description is taken was obtained by moult from an earlier stage, and the moulted skin

* From Beaufort .N. Carolina.

appears to be in exactly the same stage of development, with large chela and long antennal flagellum. One specimen moulted to post-larval, the moulted skin being almost entirely eaten up.

The larvae of these two species are almost identical in structure, but differ in the rostrum, the presence or absence of setae on the outer margin of the exopod of the maxilla, and the number of lateral spines on the telson. In colour the difference is very striking.

Post-larva 1. (Fig. 18, *a–l.*) Length 4·7 mm. without rostrum.

The rostrum is shorter than the eye, with five small dorsal teeth. The carapace has a small antennal spine, but no supraorbital nor hepatic spines. The telson is less than three times as long as wide, with two pairs of lateral spines and six terminal spines. Segment 1 of the antennule has a small spine on its outer distal angle, and a stylocerite which does not cover the statocyst; the outer flagellum consists of two thick basal segments, the second bearing a small unsegmented accessory flagellum, and a slender distal part of about six segments.

The mandible has no palp; the incisor process is pointed, without teeth, and the molar process has two parallel brushes of small spines. The palp of the maxillule has a single small inner curved process. The maxilla has two small inner lobes; an unsegmented endopod without setae, and large exopod which is not very broad in front. Maxillipede 1 has the coxa very reduced, and the basis large, but not produced; the epipod is not bilobed.

Leg 1 has the dactyl more than half the length of the palm, and the carpus a little shorter than the merus and considerably longer than the palm. The legs of the second pair are almost alike. The dactyl is very broad, flattened, with a small distal tooth and smooth inner margin fitting into a deep hollow in the propod. In the left leg there is a small peg sunk in a pit in this hollow. The propod is nearly three times as long as wide. The merus has three small blunt teeth, and the ischium two. Leg 3 is rather stouter and longer than legs 4 and 5, and leg 4 slightly shorter than leg 5. Legs 3 and 4 have three small marginal spines on the propod and a pair at the distal angle. The dactyls of these legs are rather slender, with one spine at the base of the terminal claw. Legs 1–4 retain vestiges of the exopods, and the exopod of maxillipede 3 has the apical setae reduced.

Measurements of legs (in units × about 100) :—

	Merus.	Carpus.	Propod.	Dactyl.	Total.
Leg 1	58	53	39	25	—
Leg 2 (L.)	65	29	101 × 38	38	—
Leg 2 (R.).....	68	29	117 × 38	38	—
Leg 3	76	42	61	20	199
Leg 4	65	36	55	19	175
Leg 5	70	42	61	16	189

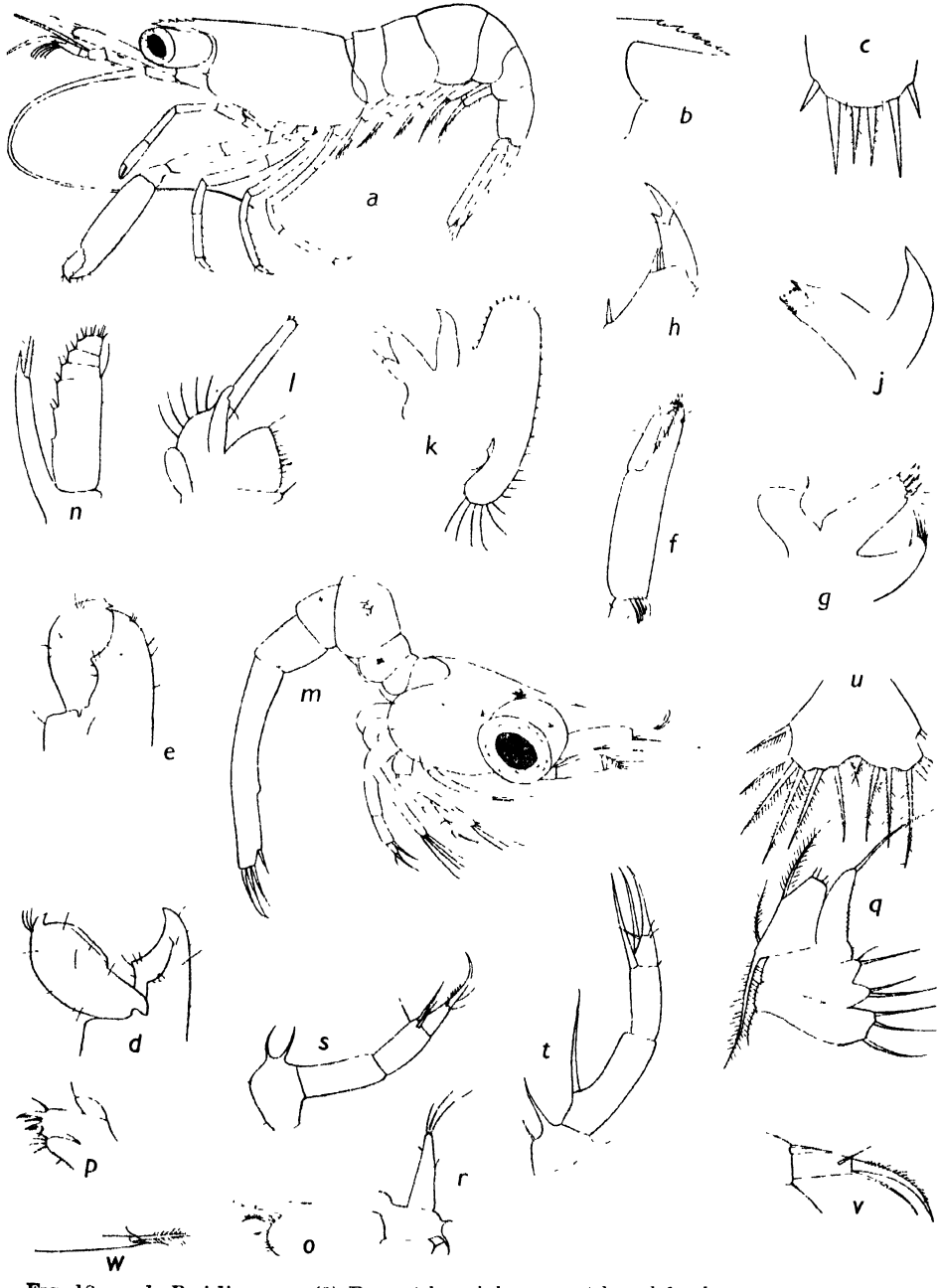

FIG. 18.—*a–l. Periclimenaeus* (?) B, post-larval 1 : *a*, post-larval 1 ; *b*, rostrum ; *c*, part of telson ; *d*, part of right chela ; *e*, part of left chela ; *f*, leg 1 chela ; *g*, maxillule ; *h*, end of leg 4 ; *j*, mandible ; *k*, maxilla ; *l*, maxillipede 1. *m–w, Periclimenaeus* sp. : *m*, Stage 1 ; *n*, antenna ; *o*, mandible ; *p*, maxillule ; *q*, maxilla ; *r*, maxillipede 1 ; *s*, maxillipede 2 ; *t*, maxillipede 3 ; *u*, telson ; *v*, Stage 2, maxillipede 2 ; *w*, antenna, endopod.

Remarks.—The close resemblance of this species, both as larva and post-larva, to *P. wilsoni* makes it reasonably certain that both belong to the same genus. We are unable to find any species throughout the whole genus *Periclimenes* which has a chela of this very peculiar form, and it seems unlikely that it would alter materially with growth. The nearest approach to it seems to be the chela of *Coralliocaris graminea* (Kemp, 1922, fig. 97). There can be little doubt that we are dealing with a species of which the adult is unknown.

The identification of the larvae here referred to the subgenus *Periclimenaeus* is not sufficiently certain to justify any deduction as to the systematic position of this group, but there can be very little doubt that the specimen which was reared to the fourth post-larval stage is correctly placed in the subgenus *Periclimenes* s. str., even if it is not certain that it belongs to *P. longicaudatus*. Its larva differs so greatly from that of *Ancylocaris* that it would seem necessary to regard *Ancylocaris* as a genus quite distinct from *Periclimenes*, the latter, so far as the larvae are concerned, being more nearly related to the *Coralliocaris* group.

PERICLIMENAEUS sp. (Fig. 18, *m–w*.). *

The adult was discovered by Mr. J. Armstrong in July 1938. It appears to be a rare species, found, associated with *Synalpheus goodei*, in a large black sponge in the shallow waters of the Reach. The species is new, and will be described by Mr. Armstrong.

The larvae were hatched in the laboratory, and a few were reared to stage 2. They are almost indistinguishable from those of *Coralliocaris* (Gurney, 1938 *b*, p. 20).

Stage 1. (Fig. 18, *m–u*.) Length 1·75 mm.

The body, in life, is bent almost at a right angle at somite 3 and the junction of thorax and abdomen. The rostrum is slender, reaching to just beyond the eye. The abdominal pleura are rounded, the telson slightly indented, the innermost pair of spines short, spines 2–5 nearly equal. The antennal scale has four distal segments, the proximal outer seta is minute, and there is a small inner papilla. The endopod has a long seta and an accessory spine.

The mandible has a three-toothed incisor process and one seta, but no well-defined molar part. The maxillule has a very small endopod with one small seta. The maxilla has an unsegmented endopod without basal lobe, or with slight indication of one (fig. 18, *q*), and five setae on the exopod. Maxillipede 1 has the endopod not protruding, with two spines, the endopod indistinctly two-segmented with three apical setae, and four setae on the exopod. Maxillipede 2 has two spines on the basis and the terminal claw fringed with spinules.

* The Palaemonid referred to on pp. 136 and 156 as a species of *Periclimenaeus* has now been described by Mr. Armstrong as *Periclimenes* (*Periclimenaeus*) *bermudensis* (American Mus. Novitates, No. 1096, p. 4, Dec. 26, 1940).

Maxillipede 3 has two spines on the basis and a very large spine at the position of the ischio-meral joint. The exopods of maxillipedes 1 and 2 have four setae. There are bilobed rudiments of legs 1 and 2.

Stage 2. (Fig. 18, *v*, *w*.) Length about 2 mm.

The carapace has no spines. The proximal seta has disappeared from the outer margin of the antennal scale, and there is a minute seta at the base of the terminal spine of the endopod as in *Coralliocaris graminea* and *Harpilius beaupresi*. Legs 1 and 2 are functional, with four setae on the exopods, legs 3 and 4 being rudimentary.

Colour.—The general colour is yellow, with red chromatophores at the base of the rostrum and eye, and yellow and brown chromatophores in the abdomen. A specimen taken in plankton at night was noted as 'very red', but with yellow ground-colour. Those hatched in the laboratory had the chromatophores very contracted.

No later stages were recognized in the plankton, but there can be very little doubt that they would be of the 'Mesocaris' form.

MESOCARIS sp. A. (Fig. 19, *a–h*.)

Last larva. Length 4·0 mm. without rostrum

The body is very much flattened and doubly flexed, the thorax being nearly as wide as long. The rostrum has no teeth, but is ridged, the ridge extending back to the end of the thorax. The carapace has a small supraorbital and antennal spine, its anterior angle being blunt. The pleura of the somites are rounded except somite 6, which has a small lateral point. The telson is long and narrow, nearly four times as long as wide, with one very small lateral spine and six terminal spines.

The mandible has a three-toothed incisor process and five setae between it and the molar part. The endopod of the maxillule is small, broad, and with one minute seta. The maxilla has the endopod simple, without basal lobe, and the exopod very broad and fringed with setae throughout. The endopod of maxillipede 1 is distinctly three-segmented and stout; the epipod is very large and bilobed. Maxillipede 2 has a large spine and a seta on the basis, and the terminal claw fringed with short spines. Legs 1 and 2 are chelate, leg 2 the larger. The setae of the propod are not plumose. Legs 1–4 have exopods with four apical setae. Leg 5 is a little longer than legs 3 and 4, without long spines on the propod, but with an inner basal spine on the dactyl.

The pleopods are large, but hidden under the large pleura.

Remarks.—The strikingly flattened form makes it possible that this is a later stage of the larva already described by one of us (Gurney, 1936 *d*, p. 621), but against this is the fact that the latter had a basal lobe on the endopod of the maxilla, and the size, which would be expected to be larger. The form of body,

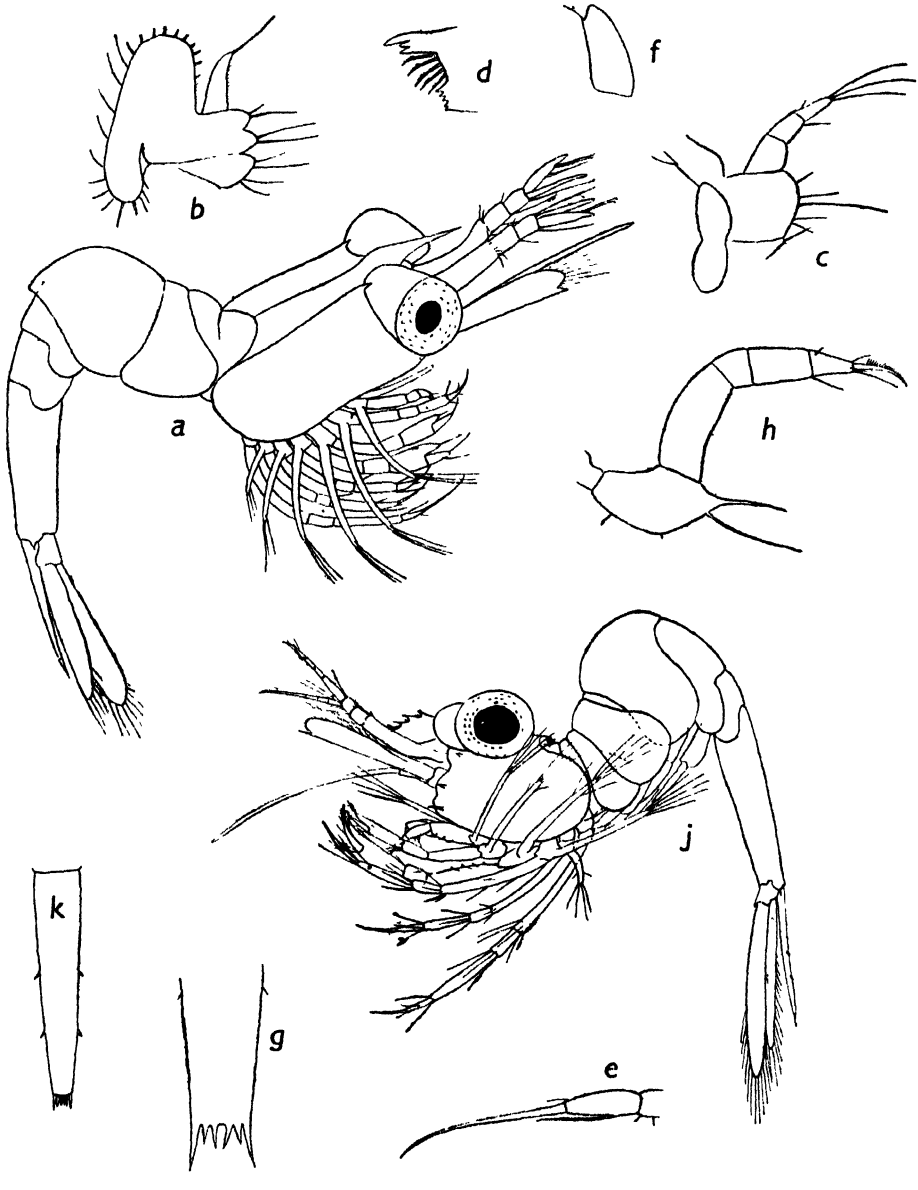

FIG. 19.—*a–h. Mesocaris* A : *a*, last larva ; *b*, maxilla ; *c*, maxillipede 1 ; *d*, mandible ; *e*, end of leg 5 ; *f*, endopod of maxillule ; *g*, part of telson ; *h*, maxillipede 2. *j–k. Mesocaris* B : *j*, *Mesocaris* B ; *k*, telson.

rostrum, and leg 5 make it fairly certain that it does not belong to the same genus as any of the larvae described above, and it is suggested as possible that it may belong to *Typton tortugae*. It is tempting to conclude from the resemblance in form of body that it is the larva of *Gnathophyllum americanum*, but of this there is no other evidence

MESOCARIS sp. B. (Fig. 19, *j*, *k*.)

This species is included because it represents an extreme case of body flexure, the bend being so great that the third abdominal somite comes near the head region, and is higher than the rostral crest. It agrees very closely with the two forms of *Mesocaris* described by Gurney (1936 *d*), especially with *M. recurva*.

It was obtained rarely in waters just outside Castle Harbour, in depths from 100 to 300 metres. The body is pink and yellow with bright pink spots in thorax and abdomen.

Larval characters of Palaemonidae in advanced stages.

PALAEMONIDAE

Supraorbital spines present. Mouth-parts somewhat reduced, endopod of maxillule and maxilla unsegmented; maxilla with three endites only.

PALAEMONINAE.

Body not flexed at junction of thorax and abdomen. Rostrum long, with dorsal teeth. Carapace with dorsal spine or spines, and usually with pterygostomial (antennal) and branchiostegal (hepatic) spines. Endopod of maxilla with or without setigerous basal lobe. Dactyl of maxillipede 2 without fringe of spinules. Legs 3 and 4 may be retarded in development. Leg 5 longer than leg 4, with basal spine on dactyl.

LEANDER (excluding L. TENUICORNIS).

Abdominal somite 3 without dorsal spine. Endopod of maxilla with setigerous basal lobe, exopod with setae on outer margin. Maxillipede 1 with small, not protuberant, basis without spines, endopod more or less distinctly segmented. Maxillipede 2 with basis not protuberant, without spines. Maxillipede 3 with one strong terminal spine on dactyl at all stages. Leg 4 with exopod (except in *L. longirostris*). Leg 5 not much larger than leg 4.

CRYPTOLEANDER (L. TENUICORNIS and allies).

Carapace without branchiostegal spine. Abdominal somite 3 without dorsal spine. Endopod of maxilla without basal lobe, outer margin of exopod

partly without setae. Maxillipede 1 with protuberant basis and endopod distinctly segmented. Maxillipede 3 with two slender spines at end in stage 1. Leg 4 without exopod. Leg 5 very much longer than leg 4.

RETROCARIS (BRACHYCARPUS and PALAEMON).

Like *Leander* except for the following differences :—

Branchiostegal spine in hepatic position. Abdominal somite 3 with large dorsal spine. Maxillipede 1 with large basis somewhat produced distally. Leg 4 with exopod. Leg 5 twice as long as leg 4, with spine on coxa.

PONTONIINAE.

Body flexed or not at junction of thorax and abdomen. Carapace usually without dorsal spine and branchiostegal (hepatic) spine. Endopod of maxilla with or without basal lobe. Dactyl of maxillipede 2 with or without fringe of spinules. Legs 3 and 4 not retarded in development. Legs 4 and 5 equal or subequal, sometimes very long. Dactyl of leg 5 with or without basal spine; coxa without spine.

Group I. ANCYLOCARIS group. (*Periclimenes* subgenus *Ancylocaris*.)

Body not flexed at junction of thorax and abdomen. Rostrum short. Carapace spines tending to disappear. Endopod of maxilla with basal lobe, exopod without setae on outer margin. Maxillipede 1 with basis protuberant, without spines, endopod usually not distinctly segmented. Leg 4 without exopod. Legs 4 and 5 subequal, very much longer than leg 3. Dactyl of leg 5 without basal spine.

Group II. MESOCARIS group. (*Periclimenes* subgenera *Periclimenes and Periclimenaeus* ; *Mesocaris* spp.)

Body more or less doubly flexed. Carapace spines usually well developed. Rostrum usually short and with toothed dorsal crest. Endopod of maxilla with or without basal lobe, exopod with or without setae on outer margin. Basis of maxillipede 1 protuberant or not. Claw of maxillipede 2 with or without fringe of spinules. Legs 3–5 equal or subequal, not elongated.

PERICLIMENES subgenus PERICLIMENES.

Rostrum small, with only one tooth. Body bent at about a right angle. Endopod of maxilla without basal lobe, exopod without setae on outer margin. Basis of maxillipede 1 not protuberant. Claw of maxillipede 2 without fringe. Legs 3 and 4 without exopods.

PERICLIMENES subgenus PERICLIMENAEUS ?

Body not extremely bent. Rostrum small, but with dorsal teeth. Exopod of maxilla without setae on outer margin, endopod without basal lobe. Endopod of maxillipede 1 with three segments, basis not protuberant. Claw of maxillipede 2 with fringe of spinules. Leg 4 with exopod.

ANCHISTIOIDES

Dr. I. Gordon (1933) in revising this genus has placed it in the subfamily Pontoniinae of the Palaemonidae instead of in the family Anchistioididae of Borradaile. From the larvae, however, it appears to be more closely related to the Palaemoninae than to the Pontoniinae (see Gurney, 1936 *b*).

(Only stages 1 and 2 of *A. antiguensis* known with certainty.)

Body slightly flexed at junction of thorax and abdomen. Mouth-parts much reduced. Carapace with posterior spine and very large branchiostegal spine. Dorsal spine on abdominal somite 3.

(Later stages presumed to belong to this genus have a very long leg 5 with peculiarly modified propod and dactyl.)

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7. The Stenopid Larvae of Bermuda. By MARIE V. LEBOUR.

Stenopus hispidus is the only adult Stenopid at present recorded from Bermuda, where it lives among rocks at low water, and is known as 'the fairy shrimp'. During a year's stay at the Bermuda Biological Station I have, however, obtained seven different Stenopid larvae, including *S. hispidus*, six from plankton in the near neighbourhood of Bermuda and one taken by the *Atlantis* from Gulf Stream water slightly further north. Of these larvae two (or possibly three) have already been recorded by Gurney (1936 *a*), who describes nine species (with a probable tenth). The number of Stenopid larvae now known from the Atlantic is therefore thirteen, and only ten adults are known to occur. Of these there are four *Stenopus*, three *Spongicola*, one *Spongicoloides*, and two *Richardina*. As will be shown below, all but one (A) of these larvae almost certainly belong to the *Stenopus* group. There must therefore be a number of Stenopids not yet discovered. *Stenopus spinosus* described by Cano (1892 *a*) from the Mediterranean, and *S. hispidus* described by Gurney (1936 *a*) are the only species whose life-history is known; none of the other larvae are attributable to any adult. In *S. spinosus* only is the post-larva described, and this, although

certain, was not obtained from a moult (Cano, 1892 *a*). For the first time it has been possible to moult the last larva of *S. hispidus* into post-larva, and also another species (B). A third (C) died whilst moulting to post-larva and was considerably damaged, although certain features of interest were seen. The whole series of larvae and post-larva of B has been secured and most of the larvae and damaged post-larvae of C, and the larval series of *S. hispidus* has been completed together with post-larva and young forms. Of the remaining forms only single or few stages were found, but of these A is specially interesting, as it is unlike any other Stenopid larva, being peculiarly primitive in certain features.

The thirteen larvae known agree in the following characters which appear to be characteristic of all Stenopids :—

They are hatched with four pairs of swimming limbs (three pairs of maxillipedes and one pair of legs).

The abdomen in the later stages is bent at the third segment at almost a right angle (as A was only seen in the first stage it is not certain if this and some of the following characters applies to it).

The endopods of the pereiopods are non-functional in the larva and the posterior pairs do not appear till late.

The rostrum is very long and the supraorbital spines prominent (except in the first stage).

The mandible is very large and fits into a deep notch in the carapace.

The telson is more or less deeply indented in the hind margin in the first and second stage and bears the usual setae seven in the first, eight in the second stage), the second being reduced to a hair.

In the later stages the hind margin is almost straight with a short spine at each angle, and six or four long setae in between.

The endopodites of legs 1 to 3 originate far from the distal end of the basipodite.

Besides these characters there are others which occur in most of the larvae :—

The abdominal pleura are pointed or produced into sharp spines on some of the somites, varying in different species (except in A and F, where they are not produced at all in any of the somites).

There is a small, simple pleopod on the first abdominal somite in the last stage of all the Bermudan species (with the possible exception of E, where it is doubtful, and A, which was only found in the first stage). In C there is one in Stage V. This is an important point, as it was not found in Gurney's specimens, and although Cano described it in *S. spinosus* Ortmann (1893) in his *Embryocaris*, which is probably the same species, states that it is absent. The probable explanation is that most if not all Gurney's specimens were earlier than the last stages. A pleopod was present on the first abdominal somite in all the post-larvae seen. In F the single specimen was in the penultimate or last stage and the pleopod was more conspicuous than in the other species.

Gurney (1936 *a*) has suggested that all the larvae having a median hooked process on the fifth abdominal segment belong to *Stenopus*. This brings in D, and probably C, the latter having a straight spine in the early stages, and a re-curved one in the last larva. His Stenopid I (1936 *a*, fig. 6) is identical with my B, and in this species there is a straight spine springing from a round prominence in the place of the procurved spine. This disappears almost entirely in the late larvae, reappearing in the post-larva. In E and F there is also a similar straight spine. Thus of all the Bermudan larvae only A is without a ventral spine on the fifth abdominal somite. It is quite possible that the early stages in the other species described by Gurney may have a spine which disappears later, and a ventral spine may thus be a characteristic of most Stenopid larvae. The mouth-parts of all the present species except A agree with those of *S. hispidus*. E was not dissected, but its likeness to the others in external features makes it almost certain that it agrees with them. In *Stenopus hispidus* and species B and C there appear to be nine larval stages, the usual number in a series where the life-history is not abbreviated.

Gurney (1924 *c*) discusses at length the relationships of the Stenopidea, and concludes that as far as the development goes they must be placed among the Reptantia, being most closely related to the Laomediidae and the higher Anomura. There is nothing in the present work to contradict this, and it is here clearly shown that there may be still further primitive characters in the larvae as in species A, and that the Stenopidea must be regarded as a very primitive group. A has a well-developed maxillule, with a setose exopod recalling the Euphausiids, the Penaeids, and some of the primitive Carids. Its maxilla is much more developed than in the other Stenopid larvae, and its antennal flagellum ends in three setae instead of two. The third maxillipedes are normal in all the larvae, but the first, second, and third pereiopods have their origin near the base of the basipodite. This is not, however, confined to certain members of the Thalassinidea and to the Anomura, but is also found in some of the Penaeids. It is well known that there are several features which the Stenopidea have in common with the Penaeidea, but all appear to be primitive, and do not necessarily indicate a very close relationship. The Stenopidea have the habits of the Reptantia, and the adults are not free swimming forms. They live among stones or are commensal with other animals, especially sponges. Most or all of the Bermudan species probably live in fairly shallow water in the adult stages, and are not truly deep water forms.

All the Stenopid larvae seen alive were very transparent, with bright red pigment in patches or spots on the carapace and centre of the abdomen, sometimes also on the antennules and telson, rarely on the rostrum. In the late larvae the grooves on the thorax and on some of the abdominal somites were frequently picked out in red. In the post-larvae there was more red, contracted by day, but expanded at night and early morning, so that the animal appeared a diffused red. In *Stenopus hispidus* even the first post-larva was coloured with broad red bands as in the adult.

STENOPID A. (Fig. 20, *a–k*.)

First Larva. (Fig. 20, *a*, *b*.) This occurs in the outside plankton a few miles from the shore in tow-nettings from 60 to 300 metres. It was only met with seven times altogether, from one to three specimens at one time, from August to September 1938, and again in June 1939. It was not seen in the winter. Length 3·5 mm. including rostrum. There is a large red patch in the thorax; otherwise it is transparent and colourless. The four pairs of swimming-limbs (three maxillipedes and first legs) are carried spread out far from the body, which is covered with very fine spicules. Abdominal pleural spines are entirely absent, and there is no ventral spine on the fifth somite. The rostrum is long, nearly a third of the length of the body including rostrum. It is unarmed and slightly arched so that the tip points downwards. The telson is deeply indented in the centre and there are no lateral teeth. The antennal scale (fig. 20, *c*) is jointed at the tip, and bears one external seta and eight setae from the tip round nearly the first half of the inner margin. The antennal flagellum bears three long setae. The mandible (fig. 20, *d*) is very large, the maxillule (fig. 20, *e*) has a rounded exopod with three setae, an unjointed endopod with four terminal setae and two pairs of internal setae, and two large setose inner lobes. The maxilla (fig. 20, *f*) has a large exopod armed with five setae, a two-segmented endopod with four terminal setae and two inner setae, and four internal lobes. The first maxillipede (fig. 20, *g*) has an exopod with four terminal setae and five-segmented endopod. The second (fig. 20, *h*) an exopod with four terminal setae and three-segmented endopod, and the third (fig. 20, *j*) four terminal setae to the exopod and four-segmented endopod. The first leg (fig. 20, *k*) has four setae on the exopod and a two-segmented endopod.

Compared with all the other larvae this species is much more primitive, and its maxillule with setose exopod and well-developed endopod strikingly different; also the well-developed maxilla with jointed endopod. Its antennal flagellum with three terminal setae also differs from all the others. The maxillule resembles that of the Euphausids, Penaeidea, and some of the primitive Carids, whilst the antennal flagellum is like an Axiid, a Dromiid or certain Pagurids. All the following species differ from A in having spines on some of the abdominal somites (except F), and a ventral spine on the fifth abdominal somite, in the reduction of the maxillule and maxilla, and in having two setae on the antennal flagellum. The mouth-parts in these agree in essentials with those of *S. hispidus* described by Gurney (1936).

STENOPID B. (Fig. 20, *l–z*; Fig. 21, *a–m*.)

This is the commonest Stenopid larva from Bermuda, occurring even more frequently than *S. hispidus*. Gurney (1936 *a*) describes, as Stenopid I (p. 387, fig. 6) a fairly late larva of this species. The stage figured by him is probably V or VII, as pleopods are present although very small, and the legs are chelate.

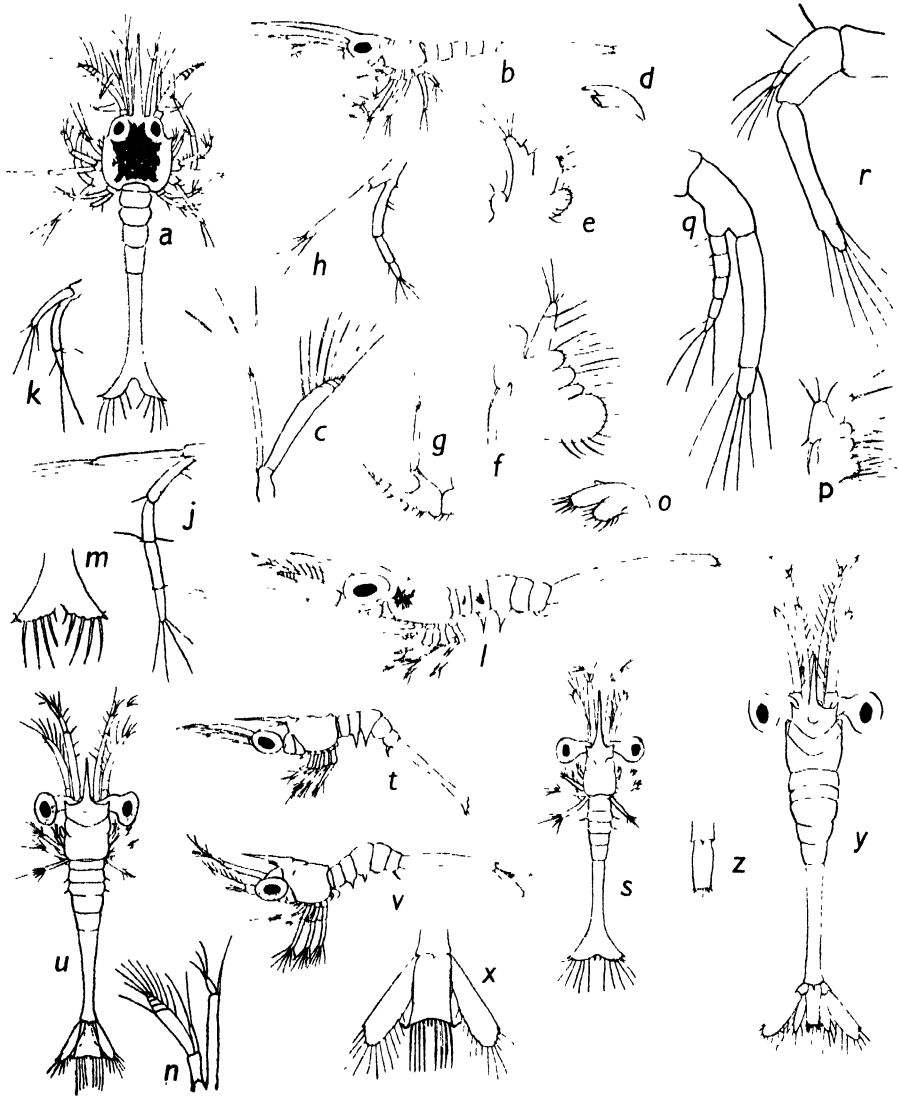

FIG. 20. *a–k*. Stenopid A, first larval stage, 3·5 mm. long. *a*, dorsal view; *b*, side view; *c*, antenna; *d*, mandible; *e*, maxillule; *f*, maxilla; *g*, first maxillipede; *h*, second maxillipede; *j*, third maxillipede; *k*, first leg. *l–r*. Stenopid B, first larval stage: *l*, first larval stage, side view, 2 mm. long; *m*, telson; *n*, antennule and antenna; *o*, maxillule; *p*, maxilla; *q*, third maxillipede; *r*, first leg. *s–t*. Second larval stage: *s*, second larval stage, 2·5 mm. long, dorsal; *t*, side view. *u–x*. Third larval stage: *u*, third larval stage, dorsal view, 3 mm. long; *v*, side view; *x*, telson. *y–z*. Fourth larval stage: *y*, fourth larval stage, dorsal view, 3·5 mm. long; *z*, telson.

His later stage recorded is slightly larger than my last stage. A complete series of larvae and post-larva from last larva has been obtained. The first stage was frequently present in plankton hauls in the Reach, taken from the Swing Bridge close to the Biological Station at night, therefore it is probable that the adult lives in shallow inshore waters, but it has never been seen. A post-larva occurred once from the same locality, and taken in the same way. Intermediate stages were always taken outside, being swept out by the currents into open water, as is the case with all the other larvae from parents breeding in the Reach. All stages of B occurred outside from a few fathoms depth to 300 metres. The early stages were common from June to August, not so frequent later, but continuing until February, after which they were not seen again until May. In the late summer and autumn the late larvae were fairly plentiful, and a post-larva was taken in December.

There appear to be nine larval stages, all of which have pleural spines on the second and third abdominal somites, and there is a straight ventral spine on the fifth abdominal somite from the first stage, which dwindles about the fifth stage, and almost or completely disappears in the penultimate and last stage, to reappear in the post-larva. This explains the fact that the spine is not mentioned by Gurney. There is a certain amount of red in the thorax congregated in one patch in the early stages, and red blotches on each side of abdominal somites 1 and 2. In the later stages there are more red chromatophores in the thorax and abdomen, and red on the last antennular segment, on the mandibles and external ramus of uropods. Grooves on the thorax and abdomen are picked out in red.

Stage I. (Fig. 20, *l.*) 1·9 to 2 mm. long. The rostrum is long, almost straight and unarmed. The body is smooth. There is no dorsal spine on the third abdominal somite. Somites 2 and 3 end in long pointed pleural spines. There is a rounded prominence ventrally on somite 5, with an almost straight, backwardly directed spine. The telson (fig. 20, *m*) is without lateral teeth, the hind margin being slightly indented. The antennular peduncle is unjointed, reaching beyond the rostrum. The antennal scale is jointed at the tip, with one external seta and eight round the tip and internal margin. The antennal flagellum bears two setae (fig. 20, *n*). The maxillule (fig. 20, *o*) has a rudimentary endopod in the shape of a small triangular process, the maxilla (fig. 20, *p*) has an unjointed endopod with two setae. The endopod of the third maxillipede (fig. 20, *q*) has five segments, that of the first leg two segments (fig. 20, *r*). The exopods of the second and third maxillipedes and first leg have six setae.

Stage II. (Fig. 20, *s*, *t.*) 2·5 mm. long. Very like Stage I, but with the eyes free, and the telson with an extra pair of inner spines. The second leg is small. The antennal scale is no longer segmented. The supraorbital spines are prominent.

Stage III. (Fig. 20, *u–x.*) ca. 3 mm. long. The telson is cut off from the sixth abdominal somite, which has a small spine. The rostrum is shorter, and the grooves on the carapace distinct. The antennular peduncle is divided into two segments. The telson (fig. 20, *x*) is longer than broad, the angle bearing a long thin spine curved inwards and upwards, and the hind margin with eight long setae and two small internal setae. The inner rami of the uropods are very small and non-setose The second leg is biramous, but without a setose exopod.

Stage IV. (Fig. 20, *y, z.*) 3·5 to 4 mm long. The base of the uropod is separate, the inner ramus setose. The second leg has a short setose exopod. Legs 3–5 are rudimentary. The antennal flagellum is not half the length of the scale. The telson is now much longer than broad, with nearly straight sides (fig. 20, *z*). It bears a small outer spine, a thick short spine internal to it, and six long terminal setae.

Stage V. ca. 4·5 mm. long. Very like IV, but the telson has lost the outer spine, and is now like all the following larval stages The third leg has a setose exopod. There are no pleopods.

Stage VI. ca. 5 to 5·5 mm. long. This is probably the stage figured by Gurney. Very like V, only with minute pleopods and the legs more developed. The ventral spine on the fifth abdominal somite has almost disappeared. The rostrum is rapidly shortening.

Stage VII. ca. 6 mm. long. The pleopods are still small. There are minute chelae on legs 1 and 2. The ventral spine on the fifth abdominal somite is absent or minute.

Stage VIII. (Fig. 21, *a, a'.*) Penultimate stage. ca. 6·5 mm. long. Legs 1–3 are chelate, 4 and 5 rudimentary, but bent at almost a right angle. The exopods on legs 1 and 2 with ten setae, on 3 with seven or eight setae. The ventral spine on the fifth abdominal somite is absent or minute.

Stage IX. (Fig. 21, *b–g.*) Last stage, ca 7 mm. long. The pleopods are longer, with one or two setae at the tips, except on the first somite, where they are minute simple buds. Legs 1–3 with ten setae on the exopods. The telson is as in Stages V–VIII. The epipods on the maxillipedes and legs 1–3 are distinct, and there are small pairs of gills on the third maxillipede and legs 1–4, one on 5. This is similar in number to *S. hispidus* (Stage IX) described by Gurney, but in the present case the gills are very short, and not nearly so well developed. The mandible has no palp, and the maxillule and maxilla have

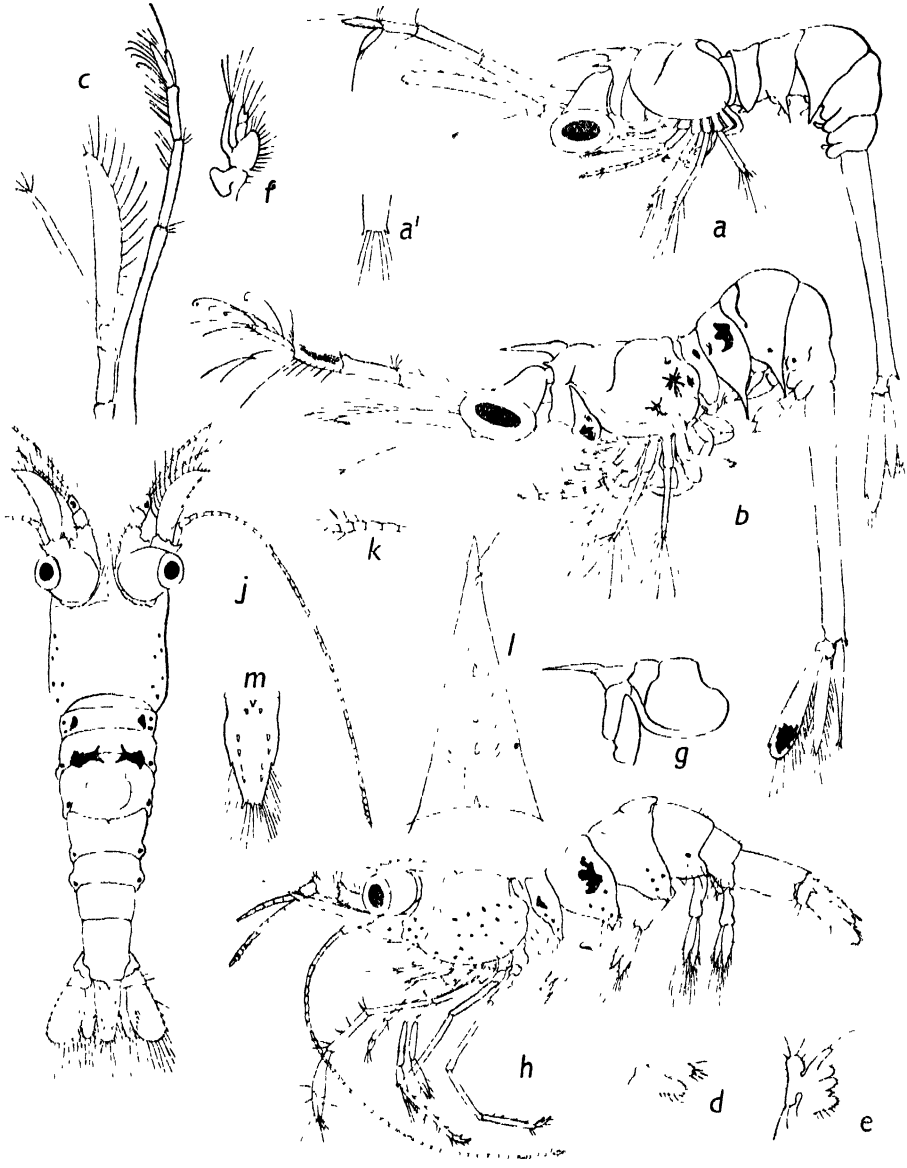

FIG. 21.—Stenopid B. a–a_1 Eighth larval stage: a, eighth larval stage, 6·5 mm. long; a_1, telson. b–g. Ninth larval stage (last): b, ninth larval stage, 7 mm. long; c, antennule and antenna; d, maxillule; e, maxilla; f, first maxillipede; g, carapace of cast skin. h–m. Post-larva, 5 mm. long: h, side view; j, dorsal; k, end of antennal flagellum; l, rostrum; m, telson.

hardly altered from stage 1, except for the larger and more setose exopod of the maxilla. This stage changed to a post-larva in a glass bowl (15/16. 11. 38). The larva lived in a finger bowl for some days, the water being changed every day, and it was fed on *Artemia* eggs which hatched out in the water.

Post-larval Stage. (Fig. 21, *h–m.*) ca. 4·6 mm. long. The body is smooth. There are red chromatophores in spots on the thorax and abdomen in the daytime, and red patches on abdominal somites 1 and 2. These enlarge very much in the dark, so that the animal flushes red. The antennular flagella are very short, and the antennal flagellum rather more than half the length of the animal. In all, the segments towards the tip are rounded. The antennal scale has teeth along the outer margin. The rostrum (fig. 21, *l*) is broad at the base, reaching almost to the end of the eye, and bears five teeth dorsally and one ventrally near the tip The abdominal pleura are all pointed, 2 and 3 ending in two teeth, 4 and 5 in one. The sixth somite is slightly shorter than 4 and 5 together. The third somite has a flattened prominence dorsally at the posterior end. The telson (fig. 21, *m*) bears a pair of lateral marginal teeth behind the centre, five pairs of teeth dorsally, and terminates in three teeth. There are long setæ round the margin from the lateral teeth round the end. The external rami of the uropods are armed with teeth on the external margin. There are remains of exopods on legs 1 3, and setose exopods on the maxillipedes. The carpus of legs 4 and 5 is undivided, and the dactyl is biunguiculate. The carpus of leg 3 is nearly as long as the merus The first pleopod is simple, but quite distinct, the second to the fifth well developed and setose. The ventral spine on the fifth abdominal somite has reappeared, and springs from a large rounded prominence. The gills are rather larger than in the last larval stage, and the posterior pleurobranchs are long, but the arthrobranchs and anterior pleurobranchs are very difficult to see, and not fully developed. There is no mandibular palp.

A second specimen was obtained which had no median spine terminally on the telson, and no dorsal spine on the sixth abdominal segment.

Stenopid C. (Fig. 22.)

The larvae of this species in stages II to IV occurred sparingly in the outside plankton a few miles off Bermuda at a depth of 80 to 300 metres. A few in the second stage occurred in the Reach in tow-nets taken from the Swing Bridge. The last stage, presumed to belong to this species on account of the pleural spines on the three anterior abdominal somites, occurred only once, from outside plankton, and unfortunately died in moulting to post-larva. All occurred in the summer. The first stage of this species was not seen, but the second resembles B very closely, differing in having the first three abdominal somites produced into pleural points instead of only the second and third, but the points do not end in true spines as in B, but are sharper in the later stages,

and the last stage has spines on somites 2 and 3. This is probably the species mentioned by Gurney (1936 *a*, p. 388) as being similar to Stenopid I, but with the first abdominal somite pointed.

Stage II. (Fig. 22, *a–b.*) 2·5 mm. long. Red at the base of the mandible, on the thorax, and at the sides of the second abdominal somite. The other stages are similarly coloured, the last having large red spots on the first three abdominal somites laterally on the last somite and on the telson. There is a sharp, backwardly directed, spine on the ventral surface of the fifth abdominal somite. The rostrum is long and unarmed, the supra-orbital spines long. The antennal flagellum has two terminal setae. Leg 2 is bilobed, but without a setose exopod. Leg 3 is rudimentary. The telson has a very shallow excavation posteriorly, and there are no teeth on the lateral margins.

Stage III. (Fig. 22, *c–d.*) 3 mm. long. The sixth abdominal somite with a median spine posteriorly, the telson with a short spine above the posterior angle, a doubly-curved hair-like spine at the angle, and eight long, and two short median spines on the hind margin. Thus it differs from B in having a spine external to the curved hair-like spine. Leg 2 has a setose exopod, leg 3 is bilobed, but simple, leg 4 a bud.

Stage IV. (Fig. 22, *f, g.*) 3·25 mm. long. The telson has a lateral spine each side at about the posterior third of its length, a short spine at each angle, and six long terminal spines. Leg 3 has a setose exopod. Legs 1 and 2 are beginning to be chelate. There are six setae on the second and third maxillipedes and legs 1–3.

Stage V. (Fig. 22, *h, j.*) 3·5 mm. long. The telson is as in IV. Legs 1–3 are chelate. The pleopods are present, simple on the first, bilobed on 2–5. Six setae on the exopods of maxillipedes 2–3 and legs 1–3. Epipods are present on the second and third maxillipedes and on legs 1–2.

These larvae are much further forward in development than the equivalent stages in B and in *S. hispidus*.

Stage IX. (Fig. 22, *k–o.*) Ca. 14 mm. long including rostrum of 4 mm. One specimen only was obtained a few miles off Bermuda, 80 metres depth, in September. This was kept alive, but died in casting to the post-larva. The figure is a composite one drawn from sketches of the living animal and its

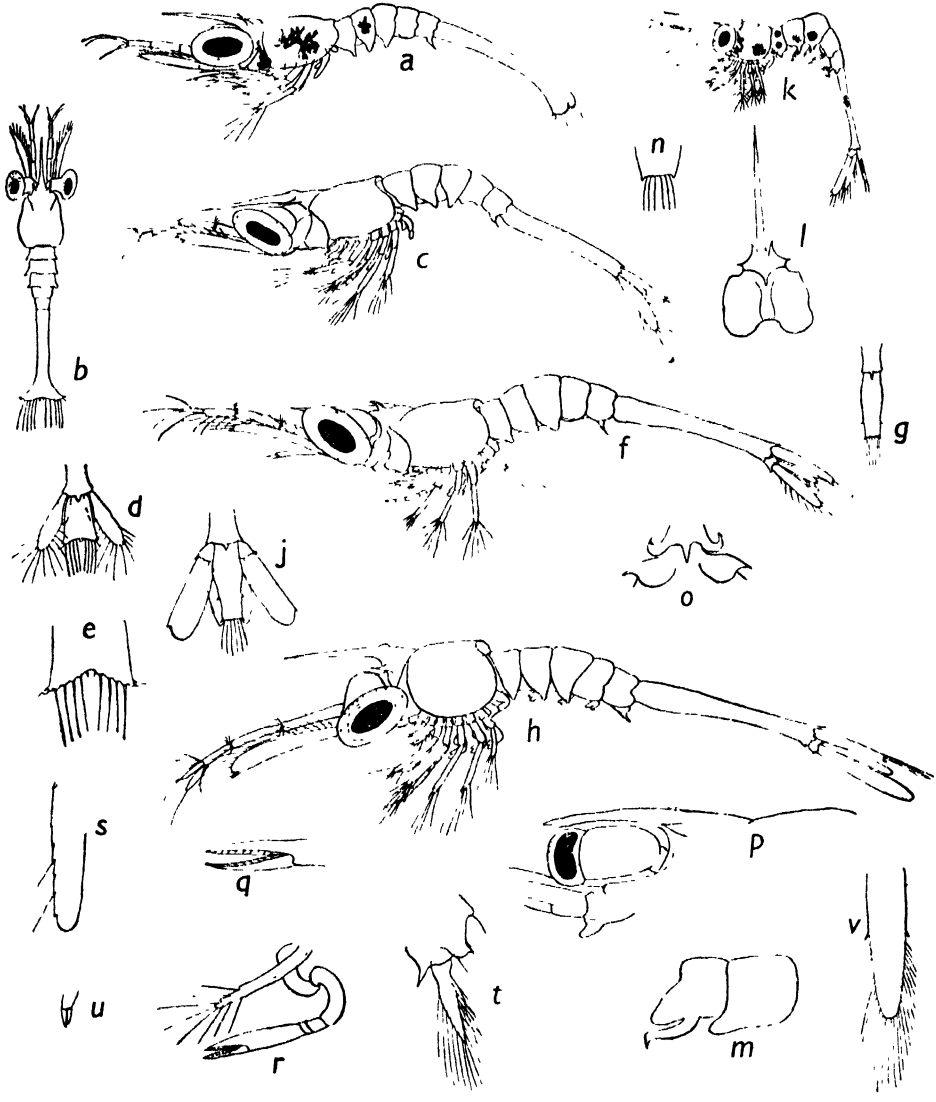

FIG. 22.—Stenopid C. *a*, second larval stage, side view, 2·5 mm. long; *b*, second larval stage, dorsal view; *c*, third larval stage, 3 mm. long; *d*, *e*, telson; *f*, fourth larval stage, 3·25 mm. long; *g*, telson; *h*, fifth larval stage, 3·25 mm. long; *j*, telson; *k*, last larval stage (rough sketch) ca. 14 mm. long; *l*, carapace of cast skin; *m*, fourth and fifth abdominal somite of same; *n*, end of telson, *o*, end of abdomen. *p–v*. Post-larva: *p*, front of post-larva from last larva (died in casting); *q*, chela of third leg; *r*, third leg with exopod of last larva; *s*, external ramus of uropod; *t*, end of fifth abdominal segment; *u*, end of last leg; *v*, telson.

cast skin. The rostrum is very long and unarmed. The ventral spine on the fifth abdominal somite is procurved, and resembles that of *S. hispidus*. There are spines on the pleura of the abdominal somites 1–3, but those on the first somite are still blunt. The sixth somite has recurved lateral spines and a dorsal spine posteriorly. There are pleopods on somites 1–5, the first very small. There are many setae on the exopods, but the skin was too much damaged for exact determination. The telson has a tooth at each angle and six long terminal setae, and a lateral tooth below the first half of its length.

Post-larva. (Fig. 22, *p–v.*) Length ca. 8 mm., but too much damaged to be certain. The following points were noted :—the rostrum is simple, with one very small tooth in front of a small knob near its junction with the carapace. The last leg appears to end in two straight claws, but this may be only from incomplete metamorphosis (fig. 22, *u*). Legs 1–3 are still twisted, and the exopod (with six setae) still attached. The chelae have a denticulated ridge on each inside margin. The third maxillipede has a setose exopod under the larval skin. There is a straight ventral spine on the fifth abdominal somite (fig. 22, *t*) and pleopods on somites 1–5, the first small and simple, the others setose. The telson has a lateral spine rather more than half way down, and beyond this there are long setae all round, the end being rounded without teeth. It is impossible to tell from this specimen whether the carpus of leg 3 is really short, as it is so crumpled up. The gills could not be made out. The body is smooth.

This species in the early stages closely resembles B, but the last larva and post-larva differ in several points. It is probable, however, that they belong to the same group.

Stenopid D. (Fig. 23, *a.*)

This is the same as Gurney's *Stenopus II* (1936 *a*, pp. 385–6, fig. 4). He also describes the first stage (1934 *c*, p. 134, fig. 54 *a*), which is of much the same type as B and C. The specimen figured by him (1936 *a*) measures 17·4 mm. including the rostrum, but is an earlier stage than one of mine of 18 mm., as it has no pleopods. He records another, length 10·6 mm., with the rostrum broken off, which has chelate legs and biramous pleopods, which is probably in the same stage as mine. Only fairly late stages occurred in the Bermuda plankton, from 100 to 300 metres, probably stages VI and VII (or VII and VIII). The largest, measuring 18 mm. including rostrum, is figured, as it differs slightly from Gurney's description. There is no dorsal spine. There is a backwardly projecting spine at the posterior angles of the carapace, and a procurved spine ventrally on abdominal somite 5, and lateral curved spines on segments 1, 3, and 4, that on segment 3 being large and projecting forwards, not backwards.

Legs 1 and 2 are chelate. There are pleopods on abdominal somites 1–5, the first small and simple, the second and third bilobed, the fourth and fifth simple. The telson has a tooth-like spine at each angle, and four long setae between. In having these four setae it resembles *S. hispidus*, all the others having six.

There are many red chromatophores on the thorax, large patches of red on the first and third abdominal segments, red on the tips of the antennules, on the eye-stalk, at the base of the mandible, at the bases of the legs, on the endopod of the third maxillipede, and at the tip of the external ramus of the uropods. The gills are hardly developed except very small epipods

Stenopid E. (Fig. 23, *b*.)

The last stage (one specimen only) was obtained by the *Atlantis* (30. 11. 38) at a depth of about 70 metres in Gulf Stream water. It was preserved, and no colour was visible. This is the smallest of all the Stenopid larvae, measuring only 4·5 mm. in length, and differs from them all in having only somites 1 and 2 of the abdomen pointed. There is a pointed ventral spine on somite 5. The rostrum is finely pointed, and reaches to the end of the first segment of the antennular peduncle, and has a conspicuous knob in front of its base. The telson has a tooth-like spine at each angle, and six long setae between. The sixth abdominal somite has a posterior dorsal spine. There are six setae on the exopods of the second and third maxillipedes and legs 1 and 2, and five on leg 3. The epipods and pleurobranchs are distinct, but the arthrobranchs very small and difficult to make out. There appear to be two arthrobranchs on the third maxillipede and on legs 1–4, and a pleurobranch on these and on leg 5, that on leg 5 the largest.

Stenopid F. (Fig. 23, *c–d*.)

Only one specimen of this species was found, taken by the *Atlantis* a few miles off Bermuda, 95 fathoms, 21. 10. 38. It appears to be in the penultimate or last stage. No colour was noted. This resembles A in having no pleural spines on the abdominal somites (except for minute spines on somites 4 and 5), but it has a straight ventral spine on the fifth segment, and the mouth-parts resemble *S. hispidus* and the other larvae, which makes it impossible that it belongs to A. The body is smooth. Length ca. 7·3 mm. The rostrum is unarmed, and reaches to the first segment of the antennular peduncle. Legs 1–3 are large and chelate. There are six setae on the exopods of maxillipedes 2 and 3 and legs 1–3. These are simple pleopods on segments 1–5, the first very small, The telson has a tooth-like spine at each angle, and six long setae between. The epipods are well developed, but not the other gills, which are hardly visible.

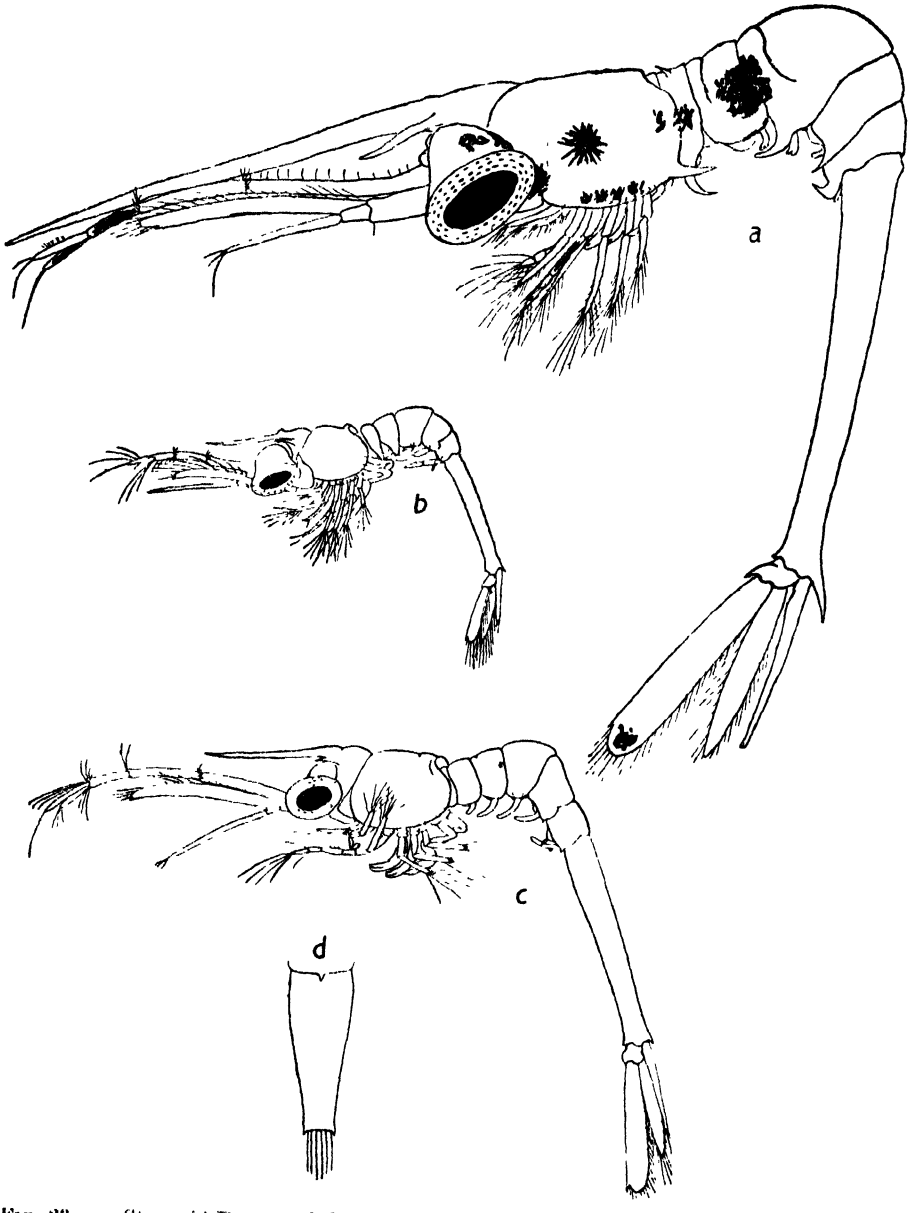

FIG. 23.—*a*, Stenopid D, seventh larval stage, ca. 18 mm. long; *b*, Stenopid E, last larval stage, ca. 4·5 mm. long. *c–d*. Stenopid F: *c*, ? penultimate stage, ca. 7·3 mm. long; *d*, telson.

STENOPUS HISPIDUS. (Figs. 24, 25, 26.)

This is the only species of the Stenopidea recorded from Bermuda, and the only Bermudan Stenopid larva of which the adult is known. Brooks and Herrick (1892) described the first larva hatched from the egg, but the later larvae attributed by them to this species belong to different genera. Gurney (1924 *c*, 1936 *a*) has discussed this species fully, and described the first larva hatched from the egg by Dr. Wheeler at Bermuda, and also the second and later larvae including the last The post-larva was not known, but I have now obtained this from the last larva. The first stage, which has frequently been seen alive, has red at the tip of the rostrum, on the antennule, thorax, first leg, third abdominal segment and on the telson There are minute spicules on the body, recalling that of species A, but these disappear in the later larvae. There appear to be nine larval stages normally as there are in B, and probably in C, but it seems that the last larva may vary much in length as larvae hardly differing at all from one another have been obtained measuring 21 mm. to 31 mm. in length, including rostrum A last larva was obtained in December 1938, which changed to the post-larva This larva measured ca. 21 mm. including the rostrum, which was 6·5 mm long. This is much shorter than the larva in the same stage described by Gurney (his specimen 31 mm long), but it agrees with it in all essentials, the chief difference being the number of setae on the exopods, the large specimens having more. As these large specimens also occur in Bermuda there seems no reason to think they are a different species.

Last larva. (Fig. 24, *a*.) 21 mm. in length, which changed to post-larva, was brightly coloured. Red on the antennule, thorax, at the bases of the legs, and on the third maxillipede, on the second abdominal somite, running into the third and at the end of the sixth abdominal somite. There is yellow on the thorax, the fourth abdominal somite, and at the end of the sixth abdominal somite. The drawing of this specimen (fig. 24, *a*) is a composite one, made from sketches of the live animal and its cast skin Other specimens vary in size (up to 31 mm.). The specimen figured (fig. 24, *b*) had no yellow pigment in the fresh preserved state, as this probably vanishes immediately after death. There are pleopods on all five abdominal somites, the first very small.

Post larva. (Fig. 24, *c*, *d*; Fig. 25.) ca. 10 mm in length. Very much like the adult at first sight, the colouring being very similar. There is much red on the body and legs, more or less in bands, with yellow in between. The antennular and antennal flagella are very long and colourless, the antennular flagella about the length of the body, the antennal more than double the length. This post-larva is much further advanced than B and C. The legs are much spread out, and the first, second and third have long remnants of exopods. The third maxillipede has a setose exopod. The rostrum reaches slightly beyond

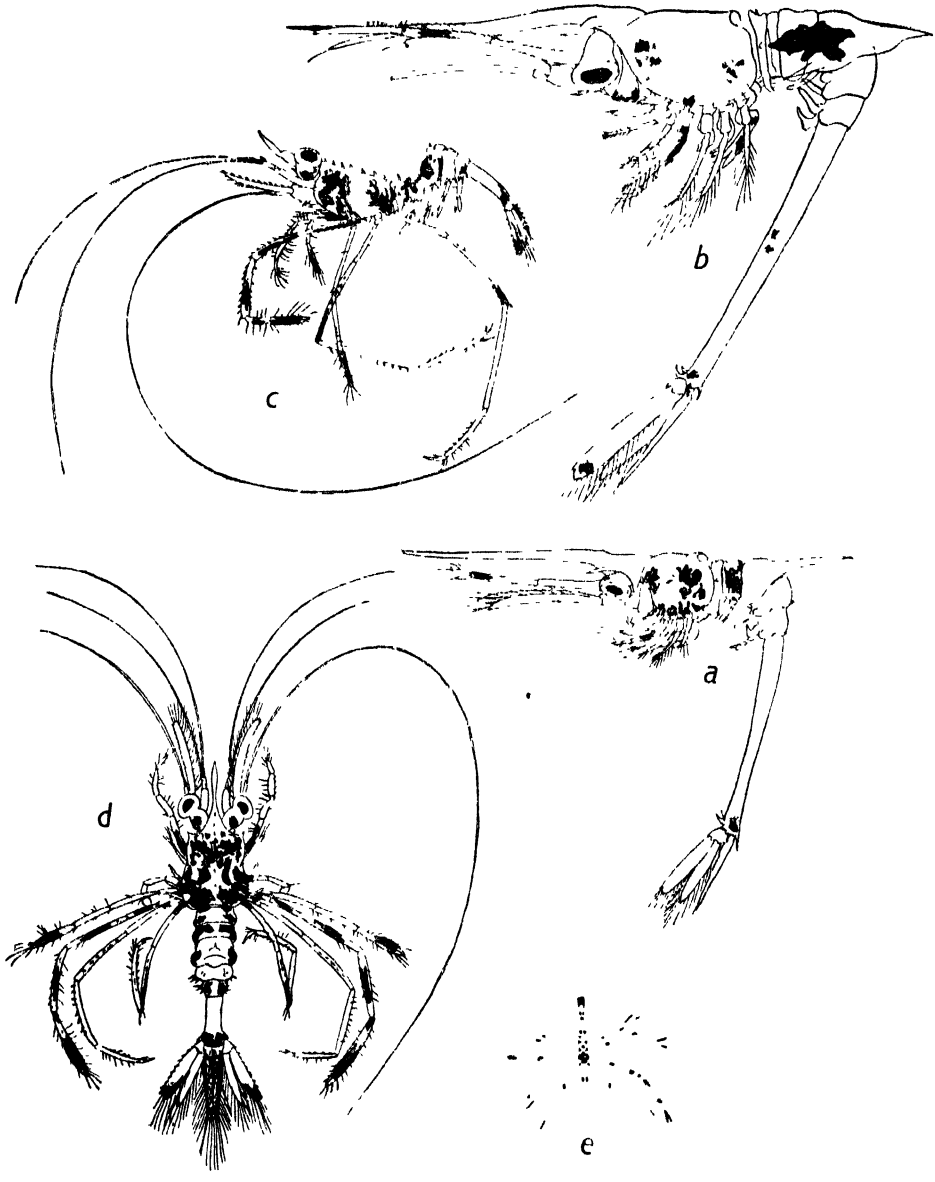

FIG. 24.—*Stenopus hispidus*. *a*, last larva 21·5 mm. long which changed to post-larva; *b*, last larva ca 31 mm. long; *c*, post-larva, 10 mm. long, from last larva; *d*, dorsal view; *e*, sketch by Dr. Wheeler of living young in bowl.

the antennular peduncle. It has a kink in the centre, which is probably abnormal, as it was not so distinct in a second specimen which died in moulting to a first young stage. It is armed at the base with three teeth, the hind one being about at the junction of the rostrum and carapace (fig. 25 *b*). There is a row of sharply curved spines dorsally in the centre of the carapace, and there are spines springing from raised knobs above the eyes. There is an antennal spine and a few other spines on the carapace. The antennal scale is about as long as the carapace, and its outer margin is denticulate (fig. 25, *c*). The first abdominal somite is pointed and bears spines dorsally and laterally, the second and third have one lateral spine pointing forwards, and the fourth and fifth end laterally in three large spines (fig. 25, *d*). The third abdominal somite bears the remains of the dorsal spine, and behind it a flat protuberance similar to that in the post-larva of B. The telson (fig. 25, *k*) bears two rows of seven dorsal spines and ends in a tooth at each angle, whilst its margin for the last two-thirds and round the end have long setae. The external ramus of the uropod is denticulate on its outer margin. There are very small, simple pleopods on the first abdominal somite and well-developed setose pleopods on segments 2–5. The exopod of the third maxillipede bears four setae, the endopod having five segments, three strong teeth on segment 2, one on 3. The first leg has a strong tooth on the merus and on the carpus, the second has one on the carpus, the third has many teeth on the merus, carpus, and propodus (fig. 25, *e–h*). The carpus and propodus of legs 4 and 5 are not segmented. The fourth leg bears five spines on the merus, four on the carpus, and several fine tooth-like spines on the merus, four on the carpus, and several fine tooth-like spines on the propodus, the fifth leg has a conspicuous hook on the coxa, six spines on the merus, and several tooth-like spines on the propodus. The dactylus in both legs is biunguiculate (fig. 25, *j*). Another post-larva, which was obtained from the plankton a few miles outside Bermuda, 300 metres, changed to a first young stage. This specimen had lost most of its legs, and both stages were much damaged during the casting, the resulting animal being dead. The length was 11 mm. The thorax and rostrum were more spiny, the rostrum bearing five teeth, still in the centre.

Later young stage. (Fig. 24, *e*; Fig. 26.) A young stage caught by Dr. Wheeler outside Castle Roads at about 80 fathoms, 28. 6. 38, also belongs to this species. He made a sketch of the colouring as it lay in a bowl showing a very definite pattern. This he has kindly allowed me to reproduce here (fig. 24, *e*). The specimen measures 32 mm. in length, and must be later than the first young stage after the post-larva, but near it. The carpus and merus of legs 4 and 5 are still unsegmented, but the body is much more spiny, and there are no traces of exopods. There are three rostral teeth still in the centre (fig. 26, *c*). The abdominal somites 2–5 end in three stout spines as in the adult.

The fact that this large young stage is so backward in development and that last larvae are found of *S. hispidus* measuring 31 mm. in length as well as small

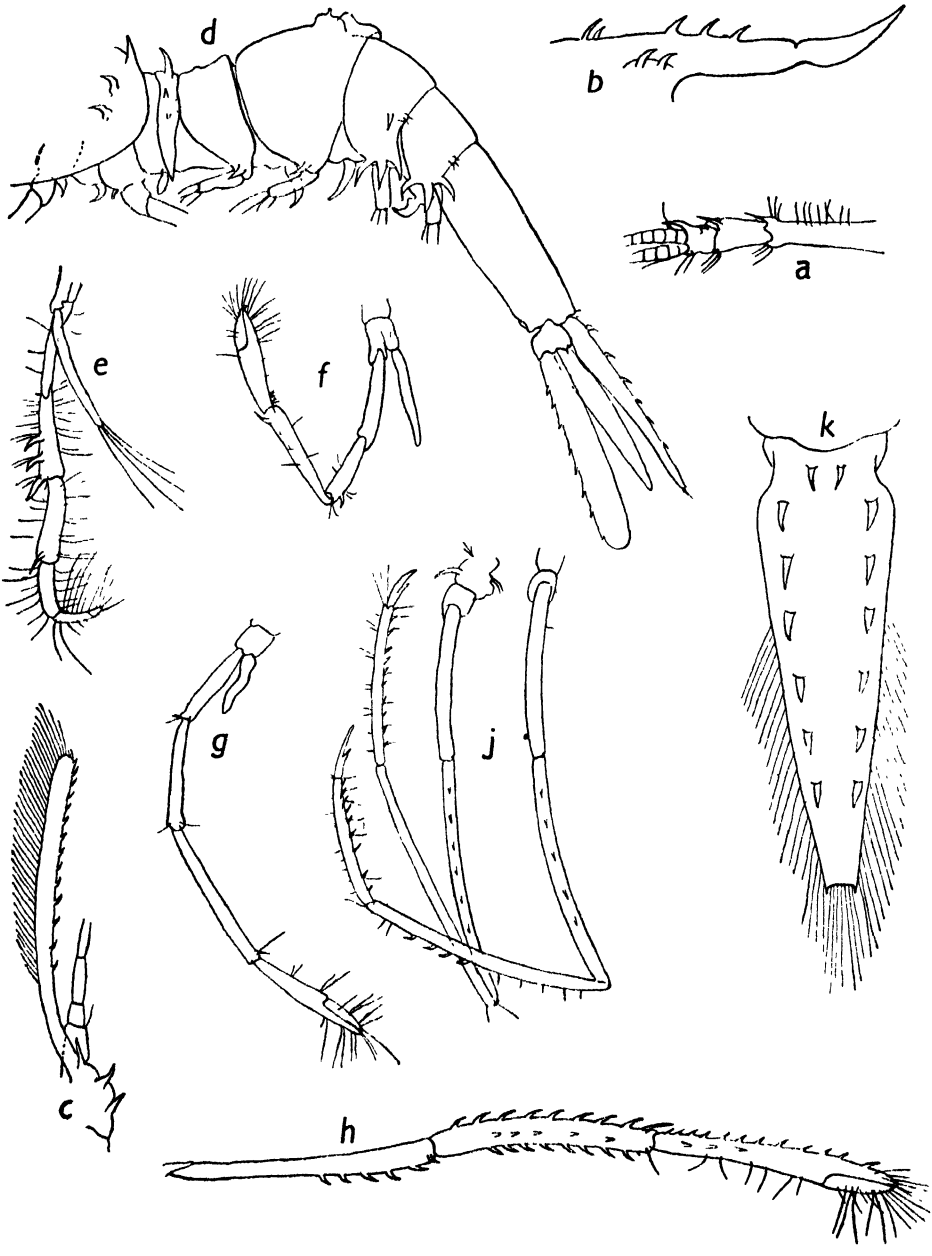

FIG. 25.—*Stenopus hispidus*, post-larva from last larva. *a*, part of antennule ; *b*, rostrum ; *c*, antenna ; *d*, abdomen ; *e*, third maxillipede ; *f*, first leg ; *g*, second leg ; *h*, third leg ; *j*, fourth and fifth legs ; *k*, telson.

specimens of 21 mm., seems to show that the last larvae differ in size because they do not all find a suitable place to metamorphose. It has been found frequently during these researches on Decapod larvae that late larvae from comparatively deep water (from 150 m. and deeper), when kept alive in bowls cast their skin only to emerge in the same form. Thus given favourable conditions the last larva (Stage IX) may change directly to a post-larva, as in the case given above, but if these conditions are not forthcoming—perhaps when the larvae are carried far out to sea—the larva may continue to change into another practically identical larva only slightly larger until more favourable conditions arise.

Comparing all these larvae it is seen that the general features are characteristic of the group Stenopidea, but each differs in some distinct way, so that no species can be confused with another. The study of the Bermudan larvae shows a much larger range of differences than was before known, and it establishes the usual nine larval stages which, however, apparently tend to multiply in the last stages if suitable conditions for metamorphosis are not available for the change to post-larva. In B we have almost certainly a coastal species whose larvae are carried out to sea, and it is the same with *S. hispidus*, which is certainly a littoral form. Species C is also found in the early stages in the Reach, and may live normally in shallow waters. The development of the larvae in the different species is not always parallel, and in C the various organs appear earlier than in B and in *S. hispidus*. All the three post-larvae obtained differ appreciably from one another, and it is, unfortunately, impossible to determine the genus of B and C, which appear to be more closely related to one another than to *S. hispidus*. It seems probable that species A, B, C, E, and F do not belong to the genus *Stenopus*, and that D is a *Stenopus* or closely related. The absence of the large dorsal spine on abdominal segment 3, present in *S. hispidus* and *S. spinosus* is rather against its being a true *Stenopus*. On the other hand, this dorsal spine occurs in many of Gurney's larvae which do not seem to be *Stenopus*, but it is absent in all the Bermudan forms, so that it may or may not be of generic importance. Species A differs so much from all the others, and is so primitive, that it most certainly must belong to something quite different from *Stenopus*—possibly to *Richardina*. The known species of *Richardina*, however, are blind, and *R. spinicincta* and *R. frederici* have very large eggs, the young hatching in an advanced stage in the former (Kemp, 1910). It cannot belong to any recorded species, and is probably new, even possibly belonging to a new genus *. B and C have setose exopods on the third maxillipedes in the post-larva, and the carpus of the third leg of B (that of C being damaged) is nearly as long as the merus, which facts would exclude *Spongicola*

* In the Report for the years 1935 and 1936 of the Bermuda Biological Station for Research, Dr. F. A. Chace records a new species and genus of Stenopidea. This was caught in Mullet Cove in the Reach in shallow water, and he tells me is probably related to *Richardina*. It is possible that this is the adult of A, or of one of the other larvae described here.

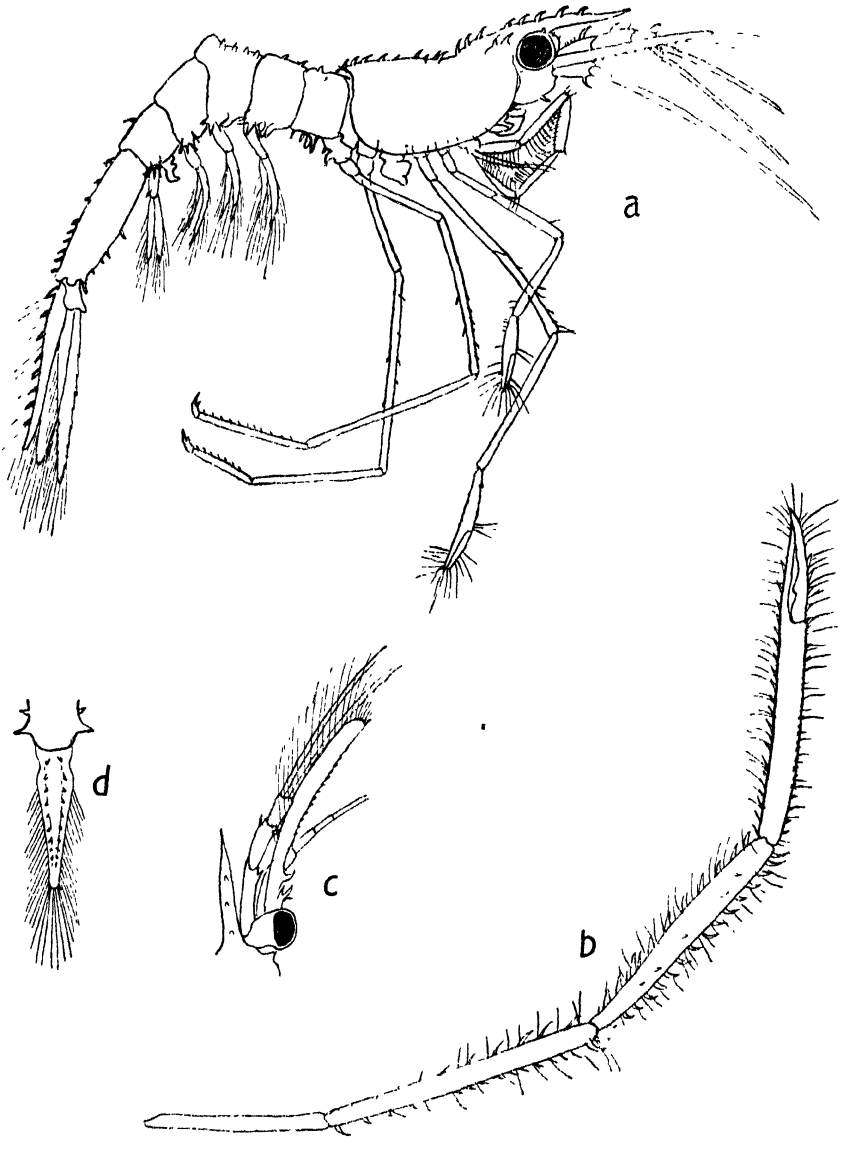

FIG. 26.—Early young of *Stenopus hispidus*. *a*, ca. 24 mm. long; *b*, third leg; *c*, rostrum; *d*, telson.

according to the table of Milne-Edwards and Bouvier (1909). In *Spongicola koehleri*, recorded by Kemp (1910) from the Bay of Biscay, the newly hatched young are very far advanced in development, and the female has large eggs. This species also is blind. The cuticle of these two post-larvae is smooth, and both are in a much less developed stage than the post-larva of *S. hispidus*. These with other distinct differences seem to indicate some other genus or genera allied to *Stenopus* or *Stenopunculus* hitherto unknown, the adults of which are yet to be discovered.

A Key to all the Stenopid larvae described by Gurney and in the present work is given below.

Key to the known Stenopid Larvae.

(Late stages only except A.)

The key is based on that given by Gurney (1936, p. 391). A–F are as used in the present paper. Gurney's larvae are indicated by the following letters :—

Stenopus hispidus	G.	Stenopid III	K.
Stenopus species II	D.	Stenopid IV	L.
Stenopus species III	H.	Stenopid V	M.
Stenopid I	B.	Stenopid VI	N.
Stenopid II	J.		

a. No spines on the abdominal pleura.
b. No median ventral spine on abdominal somite 5 ..... A
bb. A median ventral spine on abdominal somite 5 ..... F
aa. Spines on some or all of the abdominal pleura.
b. Abdominal somite 3 with dorsal spine.
c. Carapace rounded posteriorly.
d. Rostrum shorter than peduncle of antennule.. L
dd. Rostrum longer than peduncle of antennule.
e. Pleural spines on all abdominal somites ..... K
ee. Somites 4 and 5 without pleural spines ..... N
eee. Somites 2 and 5 without pleural spines.
f. Rostrum smooth or with minute spinules, somite 4 without spine ... G
ff. Rostrum toothed near end, somite 4 with minute spine .. .. H
cc. Carapace with spines at posterior angles ..... M
bb. Abdominal somite 3 without dorsal spine.
c. Carapace with spines at posterior angles ..... D
cc. Carapace without spines at posterior angles.
d. Rostrum very short ; abdominal somites 1, 4, and 5 without pleural spines. B
dd. Rostrum long ; pleural spines at least on somites 1 and 2.
e. Pleural spines on all somites ..... J
ee. Somites 4 and 5 without pleural spines C
eee. Somites 3, 4, and 5 without pleural spines ..... E

Reference.

Milne-Edwards, A., & Bouvier, E. L. 1909. Reports on the Results of Dredging under the Supervision of Alexander Agassiz in the Gulf of Mexico etc. U.S. Survey Steamer *Blake*.—XLIV. Les Pénéides et Sténopides. *Mem. Mus. Comp. Zool. Harvard*, xxvii, 3, pp. 181–274.

The Fishes of the Bangweulu Region.

By C. K. Ricardo-Bertram
(Girton College and Zoological Laboratory, Cambridge).

(With 2 Text-figures)

Introduction.

Between July 1936 and February 1937, Miss R. J. Owen and the writer were studying fishes in Lake Rukwa in Tanganyika Territory and in the Bangweulu Region in Northern Rhodesia. The collection from Lake Rukwa has already been described (Ricardo, 1939), and the present paper is an account of the fish from the Bangweulu Region. Both collections are deposited in the British Museum (Natural History).

The first part of the paper gives a brief description of the region and the fish fauna, including the geographical distribution and habits of the different species. The second part contains detailed taxonomic and ecological notes on each of the fifty-two species represented in the collection. The members of the family Cichlidæ were identified by Miss Owen and the rest of the families by myself. The taxonomic work includes descriptions of five new species.

Acknowledgements.—We should like to take this opportunity of thanking all the people who helped and advised us during our expedition; in particular Colonel and Mrs. Gore Browne, of Shiwa Ngandu, Mr. Jalland, then Provincial Commissioner at Kasama; Mr. R. Bush and Mr. T. Fox Pitt, then District Commissioners at Chinsali and Mpika; the Misses Gamwell and Mr L. Smith, of Abercorn. Among those who helped us in England, before and after the expedition, we should particularly like to record our thanks to the late Dr. C. Tate Regan, F.R.S., then Director of the British Museum (Natural History), to Mr. J. R. Norman and Dr. E. Trewavas, of the British Museum; Professor J. Stanley Gardiner, F.R.S., and Professor J. Gray, F.R.S., of the Zoological Laboratory, Cambridge; Dr. E. B. Worthington, Director of the Freshwater Biological Association; and Mr. M. Graham, of the Fisheries Laboratory, Lowestoft.

Part I.—General Description of the Region and its Fauna.

Physical Geography.

The Bangweulu Region is the source of the Congo River and it has been defined by Worthington (1933 *b*, p. 35) as the whole of the drainage basin of the Luapula River above the Mambututa Falls. These falls, situated in 12° 17′ S. and 29° 15′ E., form a partial barrier across the river and separate to some extent the aquatic fauna of the Bangweulu Region from that of the lower Luapula and the rest of the Congo. The most important waters of the Bangweulu Region are Lake Bangweulu itself, together with its vast area of swamps, the Chambezi River and its tributaries, and the upper part of the Luapula River which is the main outlet.

Lake Bangweulu is a large shallow lake lying at an altitude of 1,100 metres (3,600 feet) and with an area of open water 60 miles in length and 40 miles in width. There are several islands, the largest of which is Chilui Island lying just at the edge

of the swamps at the south-east end, while Chisi and Mbabala Islands are out in the open water. Only on the western side are there definite shores, and on the whole of the eastern and southern sides the lake merges gradually into the great swamps that cover many hundred square miles.

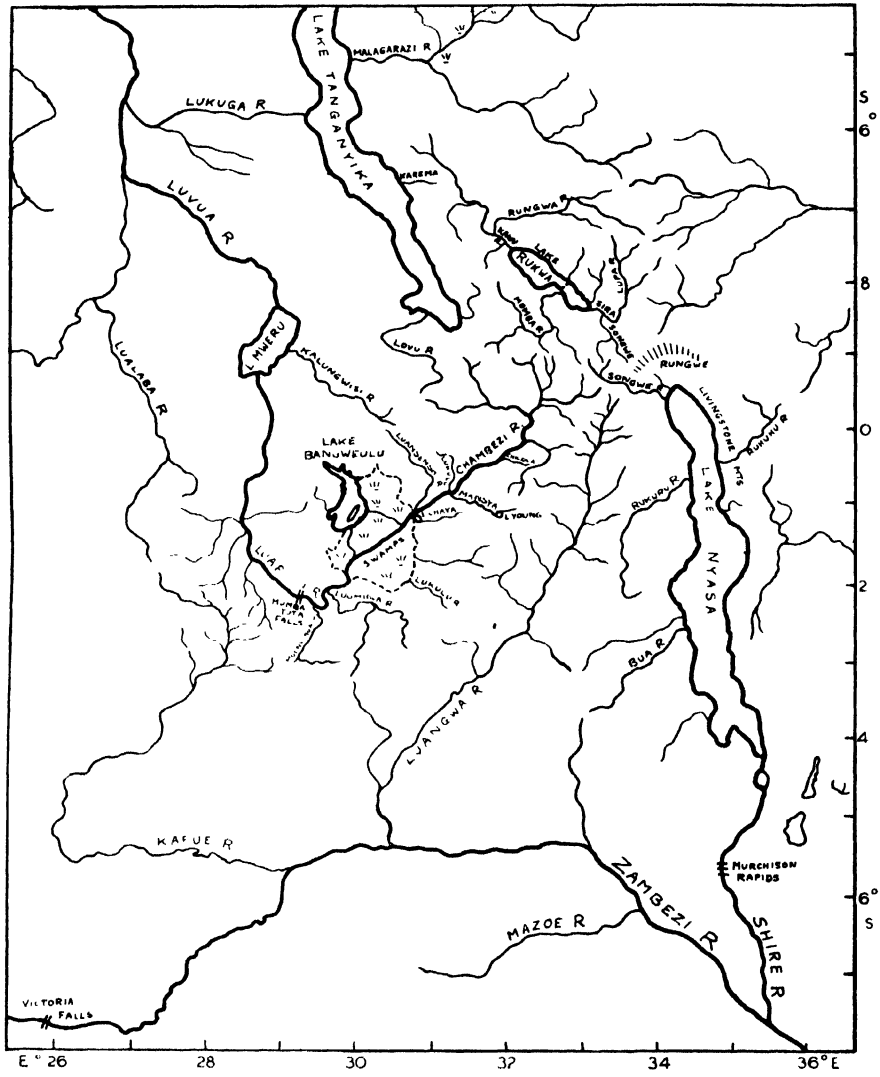

FIG. 1.—Sketch-map to show the Bangweulu Region and the neighbouring drainage systems

The Chambesi is a large river that rises just to the south of Lake Tanganyika and winds over the Northern Rhodesian Plateau for about 300 miles before it finally runs into Lake Bangweulu from a north-easterly direction. It never actually goes into the lake, but flows through the swamps to the south and finally joins up with

the Luapula River, which drains the whole area from the south end. This river flows first in a southerly direction, then swings round and runs north over the Mumbatuta Falls into the Lower Luapula and Lake Mweru and finally into the Congo.

The main tributaries of the Chambezi River are the Luansenshi, Lukulu, Mansya, Luwu, Chozi and Mumfuwe Rivers. (There is another Lukulu River that runs into the south-east corner of the Bangweulu Swamps.) The tributaries of the Luapula above the Mumbatuta Falls are the Luombwa, Mlembo and Mulnyengashi Rivers.

Lake Young is a small lake, about 4 miles long and 1 mile wide, which lies at an altitude of 1,400 metres (4,600 feet). It is drained into the Chambezi by the Mansya River.

The positions of these waters can be seen on the map on page 184. In addition to the direct connection by the Luapula River, there may also be or there may have been in the past, other connections between Lake Bangweulu and the Chambezi River on the one hand and the Lower Luapula River and Lake Mweru on the other. Some of the rivers on the west side of Lake Bangweulu come close to the easterly tributaries of the Luapula River, and the Luansenshi River of the Chambezi system rises near to the head waters of the Kalungwisi River, which runs into the east side of Lake Mweru.

The Bangweulu Region also lies near to the Zambesi system. Several of the tributaries of the Luapula (Congo system) come very close to the head waters of the Kafue and Luangwa Rivers, both belonging to the Zambezi system. Worthington (1933 *a*, p. 288) says that Captain Pitman observed a direct communication between the Luangwa and Luapula Rivers. On the divide between the two systems there is a small lake draining into the Luangwa in dry weather, but which, during the rains, also has an effluent running west into the Luapula. Worthington also points out that the watershed between the Luapula and Kafue River is swampy and that it may be sufficiently wet to allow the passage of certain kinds of fish. Even if the connections at the present time are small and scarce, it is clear that a very small change in levels or increase in rainfall would have large and far-reaching effects on the drainage and water connections of this region.

History of investigations.

The first fishes in this region were collected by Mr. F. H. Melland and the Rev. Father Foulon from Lake Bangweulu. The collection, containing 24 species, was sent to the British Museum (Natural History) in London, where it was worked out by Boulenger (1905). Further collections were made later by Mr. Melland and added to those already in the Museum. The lake, and particularly the Luombwa River, has also been visited by Belgian naturalists, who sent their specimens to the Congo Museum at Tervueren. These are described by Poll (1933) and David and Poll (1937). In 1931–32 Captain Pitman made collections over a large area of Northern Rhodesia. His fishes were identified and described by Worthington (1933 *b*), and interesting notes on the distribution of the different species are given by the collector (Pitman, 1934, pp. 315–328). By 1937 the number of fishes recorded from the Bangweulu Region, including the Luombwa River, was 55. During our expedition in 1936–37, we collected fishes in Lake Bangweulu, the south-east part of the Swamps, the Chambezi River up to the Chilolo confluence, the Mansya River and Lake Young. Our collection contains about 600 specimens, representing 52 species, 32 genera and 13 families. Five of the species are new to science and 13 had not previously been recorded from the Bangweulu Region.

The fish fauna.

There are now 67 species recorded from this region. These are listed below, together with notes on their geographical distribution.

Table of species.

Species.	Bangweulu * Region.	Congo system † (inc. Lake Tanganyika).	Zambesi system (inc. Lake Nyasa).	Elsewhere.
MORMYRIDÆ.				
Mormyrops deliciosus	‡P (C)	P	P	West Africa.
Petrocephalus simus	P (C, Bs)	P	—	Ogowe, Senegal, Chad, Niger.
Marcusenius stappersii	P (Bs, L)	P	—	—
Marcusenius discorhynchus	P (C, Bs, B, L)	P	P	Lake Rukwa.
Gnathonemus monteiri	P (C, Ch, Bs)	P	—	—
Gnathonemus macrolepidotus	P (M, C, Bs, L)	P	P	Lake Rukwa, Rovuma River, Lake Ngami.
Mormyrus caballus	P (C)	P	—	—
Mormyrus longirostris	P (C, B)	P	P	Lake Rukwa.
KNERIIDÆ.				
Kneria auriculata	P (Y)	P	—	Muza River (Mozambique).
CHARACIDÆ.				
Bryconæthrops microstoma var. *boulengeri*.	P (M)	P	—	Cameroon, Gaboon.
Alestes macrophthalmus	P (M, C, Ch, B, L)	P	—	Gaboon.
Alestes liebrechtsii	P (L)	P	—	—
Alestes imberi	P (C, Bs, L)	P	P	Rovuma and Quanza to Limpopo River.
Alestes grandisquamis	P (C, Ch, B, L)	P	—	—
Micralestes acutidens ?	P (M)	P	P	Nile, W. Africa, Limpopo River.
Petersius rhodesiensis	E ? (C, Bs, B L)	P ?	—	—
Hydrocyon lineatus	P (C, Bs, B)	P	P	Nile and Tropical Africa.
CITHARINIDÆ.				
Distichodus maculatus	P (C, Bs, B, L)	P	—	—
Nannocharax minutus	E (Bs)	—	—	—
CYPRINIDÆ.				
Barilius neavii	P (M, C)	—	P	Malagarazi River.
Barbus trimaculatus	P (C, B, L)	P	P	Transvaal, Zululand, S. Angola.
Barbus paludinosus	P (C, B, L)	P	P	E. and S. Africa from Abyssinia to Angola, Orange River, Natal.
Barbus eutænia	P (M, C, L)	P	P	Lake Kivu, Malagarazi River, Angola, Transvaal.
Barbus multilineatus	P (Bs, L)	—	P	—
Barbus vernayi	P (Bs, L)	P	—	Angola.
Barbus lornæ	E (Y, M)	—	—	—
Barbus banguelensis	P (Bs, L)	P	P (N only)	—
Barbus unitæniatus	P (C, Bs, L)	P	—	Angola, Transvaal, Zululand, Natal.
Barbus barilioides	P (Bs, L)	P	P	—
Barbus brevidorsalis	P (Y, L)	P	P	—
Barbus lineomaculatus	P (L)	P	P	E. African Rivers.
Barbus owenæ	E (B)	—	—	—
Barbus haaseanus	P (Bs, L)	P	—	—
Barbus macrotænia	P ? (L)	—	E (N only)	—
Labeo altivelis	P (C, Ch)	P	P	—
Labeo simpsoni	E (C)	—	—	—
Labeo darlingi	P ? (L)	—	P	Limpopo River.

* In column 2 the localities within the Bangweulu Region from which the various species are recorded are shown in brackets.

Y = Lake Young. M = Mansya River. C = Chambezi River.
Ch = Lake Chaya. Bs = Bangweulu Swamps. B = Lake Bangweulu.
L = Luombwa River.

Table of species (cont.).

Species.	Bangweulu * Region.	Congo system † (inc. Lake Tanganyika).	Zambesi system (inc. Lake Nyasa).	Elsewhere.
BAGRIDÆ.				
Auchenoglanis occidentalis	P (C, Ch, B)	P	–	Nile, Lake Rudolf, Lake Albert, Chad, Niger, Senegal.
Chrysichthys mabusi	P (C, Ch, B)	P	– –	–
SCHILBEIDÆ.				
Eutropius bangwelensis ...	P (Ch, B)	P	–	–
Schilbe mystus	P (C, Bs, L)	P	P	Nile and Tropical Africa.
CLARIIDÆ.				
Heterobranchus longifilis ..	P (M)	P	P	Nile, Omo, Niger, Lake Albert.
Clarias gariepinus	P (C, B, L)	P	P	Angola, S.E. Africa.
Clarias mossambicus	P (B, L)	P (T only)	P	East Africa, Abyssinia, Lake Victoria, Lake Kivu.
Clarias mellandi	P (C, Bs, L)	P	P (N only)	–
Clarias stappersi	P (C)	P	– –	–
Clarias youngicus	E (Y)		–	–
Clarias bythipogon	P (B)	P		Cameroon, Ogowe, Calabar.
Clarias theodoræ	P (C, Bs, B, L)	P	P	Angola, Natal, Zululand, Lake Ngami.
MOCHOCHIDÆ.				
Synodontis nigromaculatus.	P (C, Bs, B)	P	P	–
Synodontis ornatipinnis...	P (C, L)	P	– –	Angola.
Euchilichthys guentheri ...	P (C)	P	–	–
CYPRINODONTIDÆ.				
Aplocheilichthys mocruensis	P (Y, C, Bs, L)	P	.	– –
Aplocheilichthys katangæ ..	P (C, Bs, L)	P	–	– –
CICHLIDÆ.				
Tylochromis bangwelensis..	P (C, Bs, B, L)	P	–	–
Tilapia macrochir	P (C, Bs, B, L)	P	P	–
Tilapia melanopleura	P (C, Bs, B, L)	P	P	W. Africa, Zululand, Bechuanaland.
Tilapia sparrmanii	P (Y, M, C, Bs, B, L)	P	P	Angola, Bechuanaland, Natal.
Haplochromis philander dispersus	P (Y, M, C, Bs, B, L)	P	P	Angola, Transvaal, Bechuanaland.
Sargochromis mellandi	P (C, B, L)	P	– –	Angola.
Serranochromis angusticeps	P ? (L)	P	– –	–
Serranochromis kafuensis..	P (M, C, Bs)	P ?	P	Mossamedes, Lake Ngami ?
Serranochromis thumbergi .	P (M, C, Bs, L)	P	P	Angola, Lake Ngami.
ANABANTIDÆ.				
Ctenopoma multispinis ..	P (C, Bs, L)	P	P	Bechuanaland.
Ctenopoma nanum	P (L)	P	–	Ogowa.
Ctenopoma ctenotis	P (Bs, L)	–	P	Lukuga River.
MASTACEMBELIDÆ.				
Mastacembelus signatus ..	E (C, B, L)	–	–	–

† Where the species is recorded from either Lake Tanganyika or Lake Nyasa, but not from the rest of the Congo or Zambesi systems, the letters (T only) or (N only) are shown in columns 3 and 4.

‡ P=present, but not endemic. E=endemic to the Bangweulu Region.

Affinities of the fauna.

The geographical distribution of the species is now studied to discover the affinities of the fauna as a whole. Such a study should show the extent to which the Bangweulu Region is separated from the main part of the Congo system by the Mumbatuta Falls, and whether fish from other drainage systems have also found their way into the Region. All the data are given in the table above. This shows that there are six, and possibly seven, species peculiar to the Bangweulu Region, which means that the endemicity is about 10 per cent. The true value is probably lower, because three of the endemic species belong to the family Cyprinidæ, and parts of this family, particularly the genus *Barbus*, are in need of revision. Further work will probably show that many of the species of this genus previously thought to be endemic in various regions are really referable to more widespread species.

Among the species which occur also in other regions, 57 (or 93 per cent.) are found in some part of the Congo system below the Mumbatuta Falls Those figures, together with the low endemicity, suggest that either the Falls do not form a barrier between the Bangweulu Region and the Luapula River to many species, or that these Falls have only recently come into existence. Of the 57 species, however, 21 are not found in the Luapula River and its affluents (see Poll, 1933, and David and Poll, 1937, p. 282), suggesting that there may have been other connections between the Bangweulu Region and the rest of the Congo system. The distribution of all species within the Congo system is given in detail in the two papers referred to above. They show that among the 21 species occurring in the Bangweulu Region, but not recorded from the Luapula system, three are found in Lake Mweru, four in the Lualaba River, seven in both Lake Mweru and the Lualaba, four in the Lower Congo, and three from the Tanganyika drainage basin (including the Malagarazi and Lukuga Rivers). The data at present available thus appear to make it necessary to postulate water connections in the past between the Bangweulu Region and Lake Mweru, and probably also with lower parts of the Congo system. It has been pointed out earlier (page 185) that the head waters of the Kalungwisi River, which runs into Lake Mweru, lie very close to the source of the Luansenshi River which drains into the Chambezi River. It seems very probable that there may have been direct connections between the two areas across these rivers. It is hard to see where a direct connection with the Lualaba River could have occurred. It seems probable that further investigations will show that species from this river and other parts of the Congo system are also present in Lake Mweru or the Luapula River.

If the distribution of the 61 non-endemic species in the Bangweulu Region is further examined, it is found that 34 or possibly 35 species (56 per cent.) are present in some part of the Zambezi system. Thirty-one of these are found also in the Congo system. Among the remaining four, one is found in the Zambezi only, two are in the Zambezi and South Africa, and one is only in Lake Nyasa, but this is a doubtful record. The fact that there is a large number of fishes common to both the Bangweulu Region and the Zambezi system was pointed out by Worthington (1933 *a*, pp. 286–9, and *b*, pp. 35–7), who shows that 16 out of the 37 species then recorded from the Bangweulu Region were common to both Congo and Zambezi systems. Further, he shows that 14 were found only in the Congo, two only in the Zambesi, and five were endemic. Later collections have borne out these results, and, in spite of the number of records being nearly doubled since Worthington's figures, the proportion of the non-endemic fauna which is present in both Congo and Zambezi systems remains the same (50 per cent.).

The distribution of these fishes shows that there must have been, or must still be, a connection between the Congo and Zambezi systems. Although much of the region between the two areas has not been extensively surveyed and there is little detailed information about levels, it appears that there is no permanent connection at the present time. Pitman, however, found one place where tributaries of the Luapula and Luangwa were in communication during the rainy season. It is

probable that there are more such connections, both in this area and in other places, where the headwaters of the two systems lie close together, or where the watersheds are swampy.

There is no evidence from the fish fauna of a direct connection with Lake Nyasa. There are only three species common to the Bangweulu Region and Lake Nyasa which are not also found in other parts of the Zambesi system. Two of these are known in the Congo and one is a doubtful record. Further, there are several species from the Zambezi in the Bangweulu Region which do not occur in Lake Nyasa itself.

According to David and Poll (1937, pp. 283–4) the Zambezi system contributes a very large proportion of the fauna in the Bangweulu, Luapula, and Lake Mweru Regions. Their figures show that the combined region of Bangweulu and Luapula has nearly twice as many fish from the Zambezi as from the Congo, that Lake Mweru has slightly more from the Zambezi, and that the Lualaba has nearly four times as many from the Congo as from the Zambezi. Since Pitman's (see Worthington, 1933 *b*) and the present collections do not bear out that such a high proportion of Zambezi forms exist in the Bangweulu Region, it appears that the Zambezi specimens are mostly in the Luapula River. This suggests that the main connection between the Congo and Zambezi systems in this region was west of Lake Bangweulu, below the Mumbatuta Falls, and probably through the southern and western tributaries of the Luapula River.

To summarize: the fauna of the Bangweulu Region contains few endemic species. Most of the remaining species are found in some part of the rest of the Congo system. Not all of these have been recorded from the Luapula River, the present effluent from Lake Bangweulu into the Congo River, which suggests that there may formerly have been other connections between the Bangweulu Region and the Congo. The presence in the Bangweulu Region of a large number of fish known also from the Zambezi suggests water connections between the Zambezi and Congo systems. A small connection between the Luangwa and Luapula Rivers has actually been observed by Pitman. The evidence from the fish fauna is that the main connection was probably between the tributaries of the Zambezi and the Luapula below the Mumbatuta Falls. Before the distribution of the species on the Congo-Zambezi watershed can be fully understood, more information is needed of the fish in the Zambezi tributaries.

Distribution of species within the Bangweulu Region.

The Bangweulu Region covers a large area and contains a great variety of different water conditions. There are large and small rivers, both slow and fast running. There are hundreds of square miles of swamp country consisting of thick reeds, intersected by narrow channels of clear water. Finally, there is the large expanse of open water of Lake Bangweulu itself. (The different parts of the Region visited by us are described in greater detail on pages 192–195.) Within this large region, variations in the fauna are to be expected. Unfortunately, there are few collections from much of this country, and, apart from Captain Pitman's collection, there is usually little information about the exact locality in which any fishes were caught. The data at present available are summarized in the second column of the table on pages 186–187.

Of the total of 67 species, all but 13 are found in the Chambezi River, the Bangweulu Swamps or the lake. There are five species recorded from the Luombwa River only. Although some of these may be doubtful records (see pp. 205, 206, 213, 215), this river has 35 other species in common with the Chambezi-Bangweulu area, showing that it is fundamentally a part of this region. Lake Young and the Mansya River also contain eight species not found elsewhere in the region.

Our own collections give detailed information about the distribution of fishes in the Mansya River between Lake Young and the Chambezi. Although the Mansya

River forms a direct connection, our collections showed that there were only six species in Lake Young, whereas there are over 40 species in the Chambezi. It was known that there were waterfalls on the Mansya which flows swiftly and drops 700 feet in 50 miles. We decided, therefore, to walk along the river and find out which of these falls was effective in limiting the distribution of fish. During this journey it was impossible to make full collections at each place, and much of the information was obtained by questioning natives. The results of actual collection are shown in the table on page 194.

About three miles above the confluence with the Chambezi River there are rapids which are said to form a barrier to some species of fish, particularly the larger cichlids and mormyrids. The *Gnathonemus*, *Alestes*, *Heterobranchus*, *Tilapia*, and *Serranochromis* recorded from the Chambezi River were all taken below these rapids. Further upstream come the Senkele Falls, with a drop of about 10 feet, and these form a fairly effective barrier to the movements of fish. Above these falls only a few Chambezi species are said to occur, and our collections contained only *Barilius* and *Barbus eutænia* from that river. Between these falls and the next we also collected two species (a *Bryconæthiops* and a *Micralestes*), neither of which genera had previously been recorded from the Bangweulu Region. One further species, otherwise endemic in Lake Young, was also taken in this stretch. The next falls have a sheer drop of 20 feet through a narrow rocky valley, and these must form a complete barrier to the fish. Upstream of these falls only the fish found in Lake Young are present.

In spite of all these falls, there are three species in Lake Young that are also found in several other parts of the Bangweulu Region. It may be that these have passed the barriers coming from the Chambezi, or that they penetrated into the lake before the falls were formed. It is also possible that they came into the lake from a different source, perhaps by the Mansya River above Lake Young, or by a tributary of this river. It is hard to explain the presence in the stretch of water between the two largest falls on the Mansya River of two species not found elsewhere in the Bangweulu Region. It seems probable that further collections will show that they are really more widespread in their distribution.

It is certain that more detailed investigations are needed into the presence and distribution of fishes in the Bangweulu Region, particularly in the upper parts of the Chambezi system. These should show not only the local distribution, but should also give information as to where connections with the Zambezi system may have been.

Ecology of the fishes.

Except for three months spent on Lake Young, we were travelling more or less continuously while in the Bangweulu Region, so that it was impossible to do much detailed ecological work, and only a small proportion of the fish caught could be examined carefully. It has been possible, therefore, only to give a few indications of the life of the fish in the region. The following descriptions are based on data collected during visits to the upper part of the Chambezi River in September and November and a month (end November to end December) spent in the lower part of the Chambezi, the Bangweulu Swamps and Lake.

In studying the distribution of the different species, it at once becomes apparent that there are two distinct types of fauna, one in the swamps and one in the more open waters. The fauna of the swamps is the simpler and may be considered first.

Swamps.

The most important fishes are the mormyrids, the cichlids, the catfish *Clarias* and several small species of *Barbus*. Thus, there is not a great variety of species, but the few that are present are found in enormous numbers. The swamps form a very uniform environment, offering few different kinds of habitats for the fish, and most of the species live in the narrow channels among the weeds. The mormyrids

feed largely on insects, including water-beetles, but some had chironomid worms in their stomachs, showing that they also live on the fauna of the bottom mud. Most of the cichlids seemed to be feeding on vegetable matter, but two, *Serranochromis* spp., are predators, probably feeding on small fish and fry. *Clarias* is omnivorous and is an important scavenger. The food chains in the swamps, therefore, are simple, as the number of different species is small and the fish feed mainly on the weeds and insects of the environment, and do not depend to any large extent on one another for food.

Open waters.

It is clearly impossible to make a definite distinction between swamps and open water, and many of the fish occur in both regions. In this paper, however, the term 'open water' is used to cover any part that is not swamp, and includes the Chambezi River, Lake Bangweulu, and Lake Young. Except for Lake Young, which is considered separately, the fauna of the open waters has a much larger variety of fish than that of the swamps, and most of the species in the list on pp. 186–187 are represented. The environment also is less uniform, so that there are a number of different habitats for the fish. At the edges of the rivers and the lakes there are a number of cichlids, mormyrids, *Synodontis* and *Alestes* spp., and these are feeding on the weeds and the fauna living among them. Most of these fish are also found away from the shore, particularly the *Alestes*, which is very abundant in the open part of Lake Bangweulu. Although there are no data, it seems probable that some of the *Alestes* are feeding on the plankton and form the link in the food chain between the plankton and the large predatory fishes. Other species common in the open water are the tiger-fish *Hydrocyon*, the butter-fish *Schilbe*, and the cat-fishes, *Auchenoglanis*, *Chrysichthys*, and *Clarias*, and probably one or more species of cichlids. *Hydrocyon* and *Schilbe* are both true predators feeding on the smaller species in the lakes and rivers. *Auchenoglanis*, *Chrysichthys*, and *Clarias* are probably all omnivorous and feed on whatever they can find, including worms, insects, insect larvæ, and fish. The cichlids, with the exception of *Serranochromis* spp. which are predators, feed either on weeds, vegetable debris or phytoplankton. In this region, therefore, the food chains are more complex than in the swamps, as there is a greater variety both of fish and of sources of food, and the fish are dependent on one another to a greater extent.

Lake Young.

Lake Young has few species in its fish fauna, only three, *Tilapia sparrmanii*, a new *Clarias*, and a small *Aplocheilichthys*, being common. The *Tilapia* is extremely abundant, and was taken in large numbers round the edge of the lake. It feeds, like many species of *Tilapia*, mainly on phytoplankton and pieces of weed, but a few stomachs were found to contain remains of small fish. The *Clarias* is also common, and is the only predator in the lake, feeding mainly on small fish and tadpoles. The *Aplocheilichthys* is probably abundant, but appears to be restricted to the weeds round the shores.

There were considerable changes in the distribution of the *Tilapia* within the lake during the seven months we spent working in this region. During July, August and early September the fish appeared to live scattered over the whole lake. Although large numbers were caught near the shore, these were all small specimens, and they were rarely seen in the very shallow water. Examinations of the gonads showed that none of these fish were breeding. Unfortunately we were away on Lake Rukwa from mid-September to mid-November, but on our return the conditions were strikingly different. Large numbers of fish were congregated round the edge of the lake, the majority of which were much larger than any previously seen, and they were all found to be breeding.

The breeding habits of many cichlid species are of great interest. They differ markedly from the habits of most other families in that there is usually some degree

of parental care of the eggs and young fry. Sometimes the eggs and fry are carried in the mouth, or they may be guarded in nests. There is much variation in the habits even among *Tilapia* species, many of which have not yet been studied, and little was known about *Tilapia sparrmanii*.

In Lake Young, from November until we left the lake in January, large numbers of the *Tilapia* were congregated in the shallows, particularly where there was a sandy bottom. In these places the surface of every patch of sand was covered with circular depressions about 18 inches in diameter, hollowed out by the fish. Spawning probably occurred in these depressions, most of which contained clusters of greenish eggs. Each nest was continuously and actively guarded by one, or both, of the parents, who darted out and drove off any strange fish that dared to approach. No young fry were seen in any of the nests, but they were abundant in shoals round the extreme edge of the lake and in the grassy pools on the shore. Neither eggs nor young fry were seen in the mouths of adult fish, and it is therefore believed that this form of parental care does not exist in this species.

Apart from the information from Lake Young, very little is known about the breeding habits of fish in the rest of the Bangweulu Region. The main breeding season is said to be during the rains from November to March or April. In early December most of the specimens examined in the Chambezi River, the swamps or Lake Bangweulu were breeding, showing that at that time the season was well started. There are no other data about habits, and none of the cichlid fish were seen with nests, nor with eggs or fry in their mouths.

Part II.—DETAILED DESCRIPTIONS OF THE FISH.

Description of the localities in which the fish were caught.

The Bangweulu Region covers a very large area, so that we were not able to see the whole of it. During the five months that we were working in Northern Rhodesia, most of the time was spent at Shiwa Ngandu, and only about six weeks on the Chambezi River and Lake Bangweulu.

(1) *Chambezi River.*—The Chambezi River was visited at a number of places between the confluence of the Chilola River and Lake Chaya, a distance of about 120 miles (in September, November and December). It is a large, wide river that flows fairly swiftly, but is easily navigable in canoes in either direction. The depth varies considerably; in some parts there may be 7 metres or more of water, while in others there are occasional shallow rapids only a foot or two in depth, as at the Safwa Falls. Down most of its length the river flows through bush country, but there is generally an expanse of grassland of varying width on either side. In most places the banks are steep, but wherever there is slack water or lagoons, reeds and papyrus and typical swamp vegetation are usually found. Beyond Lake Chaya the banks begin to get lower and more indefinite, the amount of swamp vegetation increases, the main channel breaks up into a number of rather indeterminate branches and the river gradually merges into the swamp. (Stations 209, 210, 211, 212, 250, 251, 252, 260; for details see station list on page 194.)

Lake Chaya is a small lake lying on the eastern side of the Chambezi, just at the edge of the swamps. It is about four miles long and is uniformly shallow, with a depth of 4 to 4½ metres. Most of the edges are swampy and indeterminate, but on the northern side there is a definite shore, where Munkunta's village is situated. (Stations 261, 262.)

(2) *Swamps.* We travelled about 80 miles in the swamps (in November and December) on the way from the Chambezi to Chilui Island and back, but this was only in the south-eastern corner of the great swamp area. The water seemed to be uniformly shallow in this region, about 3 or 4 feet in depth. The vegetation consists of dense masses of rushes, reeds and other swamp plants, intersected by endless small channels and lagoons, either of clear water or filled with water lilies.

There are occasional islands rising out of the swamps, and these vary from being rather denser vegetation, where it is possible for a few people to land without sinking the island, to areas of real dry land with trees and villages. In all this region there is no distinct boundary between dry land and swamp and swamp and open water.

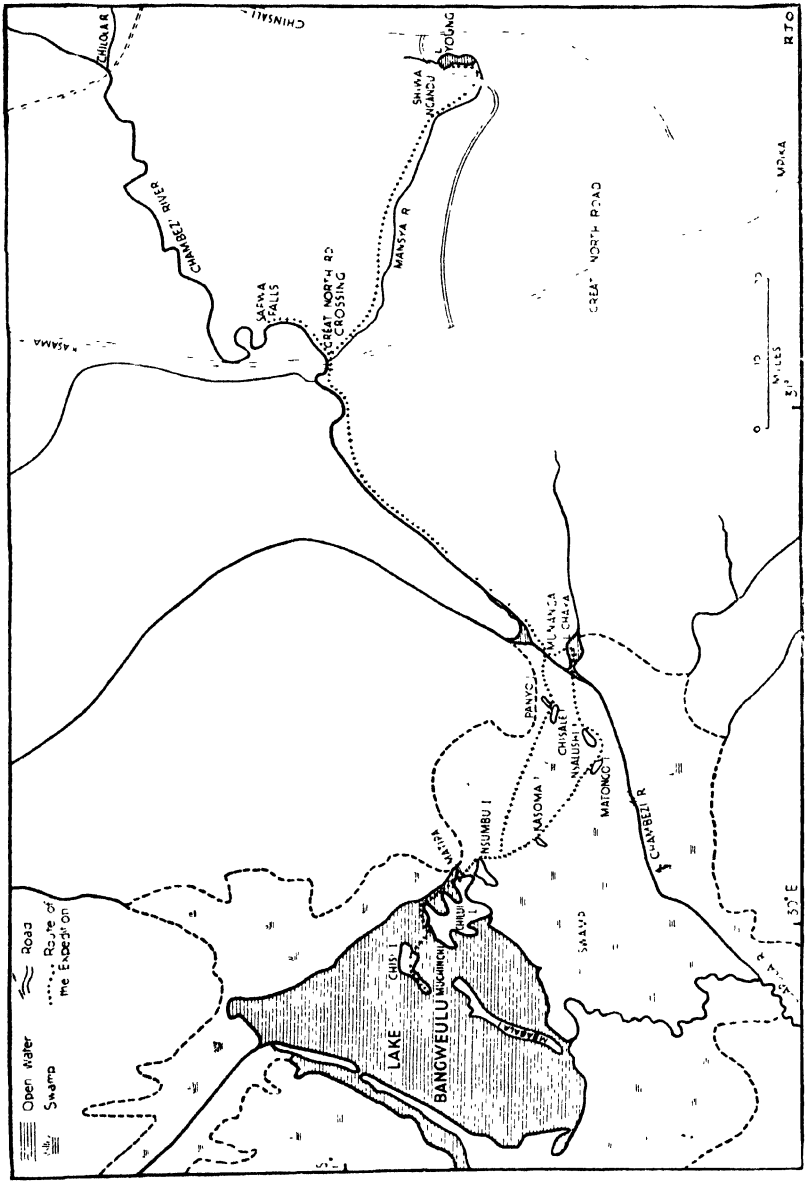

FIG. 2.—Sketch-map of part of the Bangweulu Region to show the places visited by the expedition.

On our route the swamps began near Lake Chaya and continued right across to Chilui Island. The southern and eastern sides of the island, including the village

Station list.

Station.	Locality.	Equipment.
2	Shiwa Ngandu, Lake Young, off Upper Mansya River.	2-in. gill-net.
3	,, ,, ,, ,, ,, ,, ,,	,, ,,
7	,, ,, ,, ,, ,, ,, ,,	,, ,,
11	,, ,, ,, ,, off Chitondwe.	,, ,,
12	,, ,, ,, ,, off Upper Mansya River.	3-in. gill-net.
14	Upper Mansya River, about ½ mile from lake.	Pond-net.
16	Lake Young, off Upper Mansya River.	3-in. gill-net.
17	Upper Mansya River, about 200 yds. from lake.	2-in. gill-net (short length).
20	Lake Young, off Upper Mansya River.	Dredge.
22	,, ,, near Katete River.	,,
23	,, ,, off Katete River.	2-in. gill-net.
30	,, ,, ,, ,, ,,	Dredge.
31	,, ,, off Upper Mansya River.	,,
32	,, ,, ,, ,, ,, ,,	Pond-net.
33	,, ,, ,, ,, ,, ,,	Dredge.
34	,, ,,	Line.
38	,, ,, South end of lake.	3-in. gill-net.
43	,, ,, ,, ,, ,,	Dredge.
70	Katete River, about ½ mile from lake.	Pond-net.
80	Lake Young, off Upper Mansya River.	3-in. gill-net.
	(Stations 2–43 from 30 July to 24 August, 1936.	
	,, 70 and 80 on 30 December 1936 and 14 January 1937.)	
200	Mansya River, above all waterfalls.	2-in. gill-net.
201	,, ,, above Chuswa Falls.	Lines.
202	,, ,, above 2nd falls.	,,
203	,, ,, pool below Namundela Falls.	Pond-net.
204	,, ,, below Namundela Falls.	Lines.
205	,, ,, Senkele (*a*) above Falls.	,,
	(*b*) below ,,	,,
206	,, ,, near confluence with Chambezi.	Long line.
207	,, ,, ,, ,, ,, ,, in lagoon.	2-in. gill-net.
208	,, ,, ,, ,, ,, ,, in river.	,, ,,
209	Chambezi River, above Safwa Falls.	Wuwa poison.
210	,, ,, by Safwa Falls.	2-in. & 3-in. gill-nets.
211	,, ,, below Safwa Falls.	Lines and trolling.
212	,, ,, ,, ,, ,,	Long line.
	(200–212, 4–12 September 1936.)	
250	Chambezi-Chilola confluence.	Native gill-nets.
251	Chilola River, about 1 mile from confluence.	Native gill-nets.
252	Chambezi-Chilola confluence.	Bought of natives.
	(250–252, 13–15 November 1936.)	
260	Chambezi River at Munanga, in lagoon.	3-in. & 4-in. gill-nets.
261	Lake Chaya, Munkunta.	2-in. & 3-in. gill-nets.
262	,, ,, ,,	3-, 4- & 5-in. gill-nets.
263	Bangweulu Swamps, fish-camp between Nsalushi and Matongo Islands.	Bought of natives (nets and traps).
264	Bangweulu Swamps, Chilui Island, Matipa.	Bought of natives.
265	,, ,, ,, ,, ,,	2-in. gill-nets.
266	,, ,, ,, ,, ,,	Bought of natives.
267	Lake Bangweulu, Chilui Island, Muchinchi, by weeds.	5-in. gill-net.
268	,, ,, ,, ,,	Bought of natives.
269	,, ,, Chisi Island.	,, ,, ,,
270	,, ,, Chilui Island, Muchinchi.	2-in. & 3-in. gill-nets.
271	,, ,, ,, ,, ,,	2-in. gill-net.
272	Bangweulu Swamps, Panyo, near Chisale, on path 'from the river in the sky'.	Hands.
	(260–272, 4–20 December 1936.)	
402	Lake Chila.	Small seine net.
	(January 1937.)	

of Matipa, must still be considered to be in the swamps, but the northern and western shores face directly on to the open water of Lake Bangweulu. (Stations 263, 264, 265, 266, 272.)

(3) *Lake Bangweulu.* The only part of Lake Bangweulu that we were able to visit was at the south-east end between Chilui and Chisi Islands. The distance between the two islands is about 4 miles, and over this stretch the water was about 4 metres in depth. Analyses of samples sent to the Government Chemist show that the water was fresh and contained only small quantities of mineral salts.

On the north side of Chilui Island the shore slopes very gradually and there are a certain amount of reeds growing in the shallow water. On Chisi Island, however, the shore is steeper, and in most places the edge of the lake is clear. At the south-west point of the island it is surprising to find a small patch of bare rocks standing out of the water about 50 yards from the shore. These appeared to be formed of limestone, and were the first sign of any rock that had been seen since the Chambezi. (Stations 267, 268, 269, 270, 271.)

It must be remembered that these descriptions are based on the appearance of the places towards the end of the dry season, and that they probably look very different during and after the rains. In this region the rainy season generally begins early in December and lasts till April.

Lake Young is rather shallow, with a maximum depth of about 8 metres. The entire edge is swampy, and is fringed with grasses, reeds and water lilies. There are several small streams running into it, the main ones being the Katete, Chitondwe and Mansya. (Stations 2 to 80.)

The *Mansya River* runs through Lake Young and connects it with the Chambezi River. It is a narrow, fast-running river flowing in a west-north-westerly direction from the lake to the Chambezi River. (Stations 200 to 212.)

Arrangement of data for each species.

Taxonomic.

These data are from the study of the preserved specimens that were brought back to the British Museum (Natural History) :—

(1) The name of the species is given, together with the author's name. Where a description is not included in Boulenger's 'Catalogue' (1909–1916), reference is made to the paper in which the fish is described. The native (Chiwemba or Chiwisa) name is also attempted.

(2) The specimens in the British Museum previously collected from the Bangweulu Region are mentioned, also the specimens in the Congo Museum at Tervueren, where they are of particular interest. Details of the specimens in this Museum are given by Drs. David and Poll (1937) and Poll (1933).

(3) The specimens preserved by the present expedition are enumerated, together with their lengths, the localities in which they were caught, and the station numbers. This is followed by taxonomic details of the specimens. Five new species have been described, one species has been redescribed and two nominal species have been amalgamated into one. For the rest of the species, notes have been made to show where they differ from the descriptions (in these cases the relevant part of the description is quoted in brackets for comparison). Occasionally the specimens from the Bangweulu Region are compared with those from other regions in connection with the geographical distribution of the species.

Ecological.

These data are from notes made in the field :—

(4) Notes are made on the abundance of the fish, the localities in which they were caught, and the distribution of the species in the lake. A station list, showing the methods of fishing used at each station and descriptions of the different localities, has already been given above.

(5) The results of examinations of stomach contents are given to show what the fish had been eating.

(6) Examinations of the gonads were also carried out and the sex and development were noted. The stages of development were recorded as follows: undeveloped, quiet, starting, ripening, ripe and spent.

(7) The colours of the living fish were described.

Notes on measurement of length.

In identifying and describing the specimens, the length is taken from the tip of the snout to the base of the caudal fin (i.e. standard length). Where lengths of specimens are given in figures in the taxonomic parts, these are measured in millimetres in two parts: (1) from the end of the snout to the base of the caudal fin, and (2) from the base to the tip of the caudal fin.

In the ecological parts, however, the field measurements are given, and these were recorded in centimetres as the length from the end of the snout to the tip of the caudal fin to the nearest centimetre below the actual length. In order to give true values, therefore, 1·0 cm. has been added to the upper limit wherever a range of lengths is shown.

MORMYRIDAE.

MORMYROPS DELICIOSUS (Leach). 'Mukonka'.

This species had not previously been received from the Bangweulu Region, though it is widespread in its distribution.

Only a single small specimen (215+20 mm.) was seen, and this was taken in a native fish poisoning in the Chambezi River, station 209.

All the Mormyridae are a dull grey in colour.

PETROCEPHALUS SIMUS Sauvage. 'Luwuwu', 'Buchere'.

15 specimens in the British Museum from the Lukulu River, Bangweulu Region, collected by Pitman; 14 specimens (52+11 to 110+20 mm.) were caught in the Chambezi River and the Bangweulu Swamps; one (75 mm.) from station 209, two (52 to 60 mm.) from station 252, and 11 (55 to 110 mm.) from stations 266 and 268.

These specimens are typical except that the eye is rather large: eye 3½ to 4 times in length of head (instead of 4¼ to 4½ times in the types). There are also several places where small modifications to the description must be made to include the new fish: eye 1¼ to 1½ times in interorbital width (1½ times); dorsal rays 21–28 in number (24–28); length of dorsal fin slightly less than, equal to or slightly greater than its distance from the caudal fin (equal to or slightly greater); and caudal peduncle 2½ to 3½ times as long as deep (3 times).

Worthington (1933 *b*, p. 37) has pointed out that this species is difficult to separate from the closely related species *P. bovei* (Cuv. & Val.). The separation is also made harder because some of the fish in the British Museum appear to have been wrongly identified. After examining the types of the two species in the Paris Museum, I am convinced that they must be kept distinct, and a table is given below to show the main differences.

Species.	Type locality.	Length of body over* depth.	Length of head.	Length of dorsal over * its distance from caudal.	Caudal peduncle, length over* depth.
P. simus	Ogowe	2⅞–3	4⅛	>1	3½–3⅝
P. bovei	Nile	3⅛–3¼	4⅛–4¼	<1	2⅞–2¾

i.e., divided by.

The proportion of the length of the dorsal fin to its distance from the caudal fin is very variable, and, as shown above, the specimens from the Bangweulu Regions alone have the fin longer than, equal to and shorter than its distance from the caudal. The remaining three characters (the depth of the body, the size of the head and the depth of the caudal peduncle), however, appear to be good distinguishing characters, and, using these for separation, the specimens of both species in the British Museum were examined. No changes were made in any named *P. simus*, but of the 12 specimens named *P. bovei* only two from the Rosetta Nile and Gambia appear to be true *P. bovei*, and the remaining 10 from Kaëdi, Senegal, must be considered to belong to *P. simus*.

There are no ecological data, as this species was not separated from young of *Marcusenius* in the field.

MARCUSENIUS STAPPERSII Boulenger (1915, p. 162 ; see ref. 1920). 'Mupuma', 'Luwuwu'.

This species was collected from the Bangweulu Region by Dr. Fritz Haas, but it is not represented in the British Museum collections. There are specimens from the Luombwa River at Tervueren ; 46 specimens (33+4 to 65 +10 mm.) were collected from the Bangweulu Swamps, station 266.

These fish appear to be identical to those collected by Haas and described by David (1936, p. 72). Since the original description was very brief and was based on a single specimen (65 mm.) * from the Lukinda River, Lake Mweru, and since David only makes a few numerical additions to cover Haas's fish, it is thought that a fuller description of the present specimens would be of use. It has not been possible to see either the type or Haas's fish, as they are at Tervueren. The following description is based on 12 specimens (34 +4 to 65 + 10 mm.).

Depth of body $3\frac{1}{2}$ to $3\frac{3}{4}$ times in length, length of head $3\frac{2}{3}$ to $4\frac{1}{4}$ times. Head just over 1 to $1\frac{1}{4}$ times as long as deep and $1\frac{2}{3}$ to $1\frac{3}{4}$ times as long as wide ; snout rounded, $3\frac{1}{2}$ to $4\frac{1}{2}$ times in length of head ; eye 1 to $1\frac{1}{2}$ times in length of snout, $2\frac{1}{4}$ to $2\frac{2}{3}$ times in interorbital width and $5\frac{1}{4}$ to 6 times in length of head ; mouth $3\frac{1}{2}$ to 5 times in length of head ; teeth small, 7 to 8 in each jaw ; nostrils rather nearer eye than end of snout. Dorsal 15 to 17 (17 to 19 given by David), above 4th to 9th ray of anal, 2 to $2\frac{1}{4}$ times in its distance from head. Anal 21 to 24, equally distant from base of pelvic and base of caudal or a little nearer latter, $1\frac{1}{2}$ times in its distance from head and $1\frac{1}{6}$ to $1\frac{1}{3}$ times as long as dorsal. Pectoral a little shorter than head and $1\frac{5}{6}$ to twice length of pelvic. Caudal with pointed lobes. Caudal peduncle $2\frac{1}{2}$ to $3\frac{1}{4}$ times as long as deep, $\frac{3}{4}$ to nearly once length of head. 45 to 55 scales along lateral line, $\frac{9-11}{11-13}$ in transverse series on body, $\frac{7-9}{9-10}$ in transverse series between dorsal and anal, 12 round caudal peduncle. Greyish brown in colour, lighter beneath. (This description differs from Boulenger's original one in the following three characters : caudal peduncle twice as long as deep, $\frac{2}{3}$ length of head ; scales 43 along the lateral line.)

Ecology.—There are no field notes on this species, as it was not distinguished from *Petrocephalus* or the other *Marcusenius* in the field. A number of the preserved specimens, however, have been examined. Twelve of the larger fish were opened ; all but two were preparing to breed, and three of these were females with ripening ovaries. Four stomachs were examined ; one contained algæ, cladocerans, copepods, heads of coleopterous larvæ and other insect remains ; two contained largely cladocerans, insect remains and a few nematode worms ; and one contained ostracods in addition to cladocerans and insects.

MARCUSENIUS DISCORHYNCHUS (Peters). 'Chimpumwe', 'Chipumamabwe', 'Luwuwu', 'Ntongwe'.

Three specimens in the British Museum from Lake Bangweulu, collected by Melland ; 9 specimens (105+18 to 154 +28 mm.) were collected from the Chambezi

* To the end of the middle rays of the caudal fin.

River, the Bangweulu Swamps and Lake Bangweulu : one (110 mm.) from station 209 ; 6 (110 to 154 mm) from stations 263 and 266, and 2 (105 to 110 mm.) from station 268.

These specimens fit into the description except that the following head measurements are slightly different : length of snout $3\frac{1}{2}$ to 4 times in length of head ($3\frac{1}{2}$ times) ; eye $1\frac{1}{2}$ to $1\frac{2}{3}$ times in interorbital width ($1\frac{1}{2}$ times). In one specimen of 140 mm. there are only 25 rays in the dorsal fin (30–36), but in all other characters it appears to be typical. The interorbital in the specimens from Lake Rukwa is also rather wide.

Ecology.—This fish was not at all common and was always caught in the same localities as the more abundant *Gnathonemus* spp. One specimen of 15 cm. was a female with a ripe ovary, but there are no other data about either breeding or feeding habits.

GNATHONEMUS MONTEIRI (Günther). 'Lombolombo', 'Muntesa', 'Nchesu', 'Nkupe'.

One specimen in the British Museum from Lake Bangweulu, collected by Melland ; 7 specimens (99+20 to 250+40 mm.) were collected from the Chambezi River, Lake Chaya and the Bangweulu Swamps : one (173 mm.) from station 252, one (223 mm.) from station 261, and 5 (99–250 mm.) from stations 263, 264 and 266.

These fish are typical, except that in the largest specimens (225 to 250 mm.) the eye goes $2\frac{1}{4}$ times into the length of snout ($2\frac{1}{2}$ to 3 times), the anal fin is rather nearer the caudal than the pelvic fin (equally distant), and the caudal peduncle is $2\frac{2}{3}$ to 3 times as long as deep (3 times). In the two smallest fish the teeth are conical (teeth notched).

Ecology. This species was not distinguished from the following one in the field, so that all ecological data are based on both species and are considered later.

GNATHONEMUS MACROLEPIDOTUS (Peters). 'Muntesa', 'Lombolombo'.

Three specimens from Lake Bangweulu in the British Museum, collected by Melland, and many from the Lukulu River and Changola, collected by Pitman ; 29 specimens (60+10 to 260+35 mm.) were collected from the Mansya River, the Chambezi River and the Bangweulu Swamps : one (178 mm.) from station 207, two (143 to 260 mm.) from station 251, 21 (60 to 95 mm.) from station 252, and 5 (65 to 185 mm.) from stations 263, 264 and 266.

All these specimens fit into the description except the largest, which is too deep in the body and has too long a dorsal fin, as shown by the following figures : depth of body $3\frac{1}{4}$ times in length ($3\frac{1}{3}$ to 4 times), dorsal fin with 27 rays (23–25), and length of dorsal fin twice in its distance from the head (about $2\frac{1}{2}$ times). The number of scales along the lateral line is high, 62–66 (50–69), in common with all the previous specimens from N. Rhodesia. There are 12 scales round the caudal peduncle.

Ecology.—Gnathonemus spp. are abundant in this region and were seen in large numbers in Lake Chaya and the Bangweulu Swamps. A few were also taken in the Chambezi River. At practically every station where *Gnathonemus* was caught both species seemed to be represented. These fish are important from an economic point of view, as they are rich in oil and provide a valuable supply of food for the natives.

The range of lengths for 40 specimens was from 12 to 56 cm., and the weight of 9 (25 to 31 cm.) was from 130 to 180 gm. The gonads of 13 fish were examined and they were all developing. Ten (22 to 30 cm.) were females, 9 with ripening or ripe ovaries, and one with its ovary spent, while the remaining 3 (32 to 49 cm.) were males with ripe testes.

Examination of 5 stomachs showed that the fish had been feeding among weeds and near the bottom, as they contained insect remains, chironomid worms, pieces of weed and vegetable debris.

MORMYRUS CABALLUS Boulenger. 'Lombolombo'.

This species had not previously been recorded from the Bangweulu Region, but it was known from the Upper and Lower Congo. One small specimen (77+10 mm.) was collected from the Chambezi River in a native fish poisoning, station 209.

With specimens of this size it is impossible to distinguish this species from the closely related *M. ovis* Boulenger, also from the Upper Congo, even though the types of the two species were examined at Tervueren. Most of the measurements for separation depend too much on the size of the fish to be of any use, but examination of the numbers of rays in the dorsal and anal fins, the position of the dorsal with regard to the pelvic fins and the number of scales below the lateral line in transverse series in the new specimen suggest that it is *M. caballus*. There are, however, 16 scales round the caudal peduncle, as in *M. ovis*, instead of 12–14, as in *M. caballus*.

MORMYRUS LONGIROSTRIS Peters. 'Lombolombo', 'Chipalala', 'Mbuwu'.

Two specimens from Lake Bangweulu in the British Museum, collected by Melland; 2 specimens (210+28 to 300+45 mm.) were collected in the Chilola River, stations 251 and 252.

These specimens fit into the description except that the eye is slightly small and there are too many dorsal rays. The measurement for the eye into the interorbital width is $1\frac{2}{3}$ to 2 times ($1\frac{1}{2}$ times), but this figure depends on the size of the fish, and may reach as much as three in large specimens from Lake Nyasa. The new fish have 76–79 rays in the dorsal fin, and Melland's have 78–82 rays (65–75), but this seems to be a variable character within the species, as specimens from Lake Nyasa have only 63–64. (Worthington, 1933 *a*, p. 297.)

Ecology.—This fish does not seem to be common, and only 5 were seen, 2 small ones from the Chilola River and 3 very large ones (63 to 68 cm.) from the Bangweulu Swamps at Matipa. Like all the mormyrids, it contains large quantities of oil and fetches high prices in the dried fish trade.

One fish (63 cm.) weighed 2·5 kg. The gonads of the two largest fish were examined and they were both males starting to breed.

Two stomachs were examined and found to contain chironomid worms, remains of other insects and larvæ, shrimps, pieces of weed and vegetable debris.

KNERIIDÆ.

KNERIA AURICULATA (Pellegrin).

There are no previous records of this family from the Bangweulu Region. A single specimen (49+11 mm.) was collected in the Upper Mansya River about a mile above where it runs into the north-east end of Lake Young, station 14.

This fish appears to be similar to the specimens in the Congo Museum from Katanga, described by Poll (1933, p. 116) as *Xenopomatichthys*. The number of scales along the lateral line is rather high, 90–92, but Poll has shown that this number is variable and ranges in different localities from 60 to 90, and that some of the specimens from near Elizabethville have from 85 to 90. Dr. Trewavas (1936, p. 65) suggests that this variation is so large that the species should be subdivided into subspecies and that the group containing the highest number of scales comes near to *K. polli* Trewavas from Angola. There are specimens of both species from Elizabethville at Tervueren, and until these can be examined it is thought best to regard the present specimen as *K. auriculata*.

CHARACIDAE.

BRYCONAETHIOPS MICROSTOMA BOULENGERI Pellegrin.

This species had not previously been recorded from the Bangweulu Region. Two small and badly damaged specimens (78 to 79 mm.) * from the Mansya River, station 205.

* Without caudal fins.

These fish appear to be typical except that the eye is rather small: eye $3\frac{1}{4}$ times in length of head and its diameter is slightly less than the length of the snout. The description says that the eye goes $2\frac{1}{2}$ to $3\frac{1}{4}$ times into the length of head, but since the present specimens are small, it is clear that their eye is proportionately smaller than in most specimens. In specimens from Elizabethville at Tervueren the diameter of the eye is slightly greater than the length of snout.

The larger of the specimens was a female with a ripening ovary. It was surprising to find that such small fish were mature, because members of this species grow to a much larger size (up to 150+25 mm.).

ALESTES MACROPHTHALMUS Günther. 'Mobanse', 'Lumanse'.

Two specimens from Lake Bangweulu in the British Museum, collected by Melland; 5 specimens (125+35 to 240+50 mm.) were collected from the Mansya River, Chambezi River, Lake Chaya and Lake Bangweulu; one from each of the following stations: 206, 252, 261, 268 and 269.

All the specimens fit into the description.

Ecology. This fish is abundant in the Bangweulu Region, particularly where there is open water, but it was rarely seen in the swamps. It is caught in considerable numbers in the open lake by native fishermen using lines baited with dragonfly and other nymphs.

The range of lengths for 43 specimens was from 16 to 40 cm., and the weights of 8 fish (26 to 40 cm.) were from 160 to 580 gm.

The gonads of 4 specimens (33 to 40 cm.) were examined: all the fish were females, 3 with ovaries starting to develop and one with the gonad spent.

Examination of 7 stomachs showed that these fish were feeding mainly on pieces of weed, beetles and other insects.

In colour it is silvery all over the body and the fins are grey.

ALESTES LIEBRECHTSII Boulenger.

There is one specimen at Tervueren from the confluence of the Luapula and Luombwa Rivers, but there are none from this region in the British Museum or in the present collection.

ALESTES IMBERI Peters. 'Lumene', 'Lusaku'.

One specimen from Lake Bangweulu in the British Museum, collected by Melland; 3 large (150+ ? to 160+35 mm.) and 7 small (50+15 to 100+20 mm.) specimens collected from the Chambezi River and the Bangweulu Swamps: one (150 mm.) from station 211, one (100 mm.) from station 251, 7 (50 to 155 mm.) from station 252 and one (160 mm.) from station 266.

These fish are all typical.

Ecology. This species is very common all over the region, particularly in the more open water, and it was sometimes seen in shoals at the edge of rivers.

The range of lengths of 16 specimens was from 12 to 22 cm., and the largest weighed 100 gm. The gonads of 5 fish (17 to 22 cm.) were examined and they were all females with ripening or ripe ovaries. One fish of only 12 cm. from the Chilola River also had a ripe ovary.

One stomach contained pieces of weed.

In colour it is silvery with a large black spot on the caudal peduncle.

ALESTES GRANDISQUAMIS Boulenger. 'Mutungulwe', 'Chipama', 'Mutula', 'Talala'.

One specimen from Lake Bangweulu in the British Museum, collected by Melland, and there are specimens at Tervueren from the confluence of the Luapula and Luombwa Rivers; 5 specimens (90+ ? to 265+55 mm.) were collected from the Chambezi River and Lake Chaya: one (90 mm.) from station 209, three (95 to 105 mm.) from station 252, and one (265 mm.) from station 262.

These fish are typical.

Ecology. This *Alestes* does not seem to be very common, though small specimens were seen swimming at the edges of rivers. They can easily be distinguished in the field from the other two species as the caudal fin, and often the underpart, of the body are bright pink.

The range of lengths for 8 specimens was from 9 to 34 cm. There are no data about feeding or breeding habits. One stomach was filled with kassava, but this had probably been thrown into the river by natives for bait.

? MICRALESTES ACUTIDENS (Peters).

No *Micralestes* previously recorded from the Bangweulu Region ; 2 small and badly damaged specimens (58 + ? to 63 + ? mm.) from the Mansya River, station 205.

These fish were bought off small native boys, and are so badly damaged that it is impossible to identify them with certainty.

PETERSIUS RHODESIENSIS, sp. nov.

Depth of body 4 to 4½ times in length, length of head 4 to 4¼ times. Head twice as long as broad, considerably longer than deep, lower jaw projecting slightly beyond snout ; snout shorter than eye, which is 2⅓ to 2¾ times in length of head ; interorbital width about 3 times in length of head ; maxillary extending to below anterior border of eye ; outer praemaxillary teeth 4 to 6, alternating with those of inner row, 8 in number ; 6 to 8 teeth in lower jaw. Gill rakers short, 16 to 17 on lower part of anterior arch. Dorsal II 8, originating behind vertical of base of pelvic, at equal distance from anterior border of eye and from caudal. Adipose fin very small. Anal III 16 to 17. Pectoral a little shorter than head, not quite reaching pelvic. Caudal deeply forked. Caudal peduncle 1½ to 2 times as long as deep. Scales 33-36 $\frac{5\frac{1}{2}}{3\frac{1}{2}}$, 1½ between lateral line and root of pelvic. Silvery, with a darker lateral band.

This species is very close to *P. tangensis* Lönnberg from the Tanga River, Usambara, Tanganyika (two of the types are in the British Museum), but differs in having a longer and thinner body and fewer scales in the vertical series across the body.

This description is based on 4 specimens collected from the Chambezi River, the swamps and the edge of Lake Bangweulu : one from station 252, two from 266 and one from 268 (33 + 9, 33 + 9, 42 + 12 and 43 + 12 mm. respectively). The description should probably include 14 specimens (45 to 50 mm.*) at Tervueren from the confluence of the Luapula and Luombwa Rivers (David and Poll, 1937, p. 210). These have been named *P. tangensis*, but they are similar to the present specimens in that they have a long thin body (depth 4 to 4½ times in length). There has not been an opportunity of examining these fish, but it is probable that they belong to this new species and are distinct from *P. tangensis*.

PETERSIUS, sp. ?

There are also 4 small specimens (17 + 5 to 24 + 7 mm.) collected from the Chambezi River, station 252. These are very similar to the species described above, but the body is less elongated and there are fewer scales both in the horizontal and vertical series. (Scale count 26, $\frac{4\frac{1}{2}}{3\frac{1}{2}}$, 1½.)

HYDROCYON LINEATUS Bleeker. Tiger-fish. 'Manda', 'Mchenc'.

There are 6 specimens in the British Museum from the Bangweulu Region, four collected by Melland and two by Pitman ; 4 specimens (190 + 50 to 390 + ? mm.) from the Chambezi River and the Bangweulu Swamps : one from each of the stations 207, 209, 250 and 266 (200 mm., 240 mm., 390 mm. and 190 mm. respectively).

They all fit into the description.

Ecology. This species is common wherever there is open water, but it was rarely seen in the swamps. It was caught in considerable numbers both in nets and by trolling in the Chambezi River, Lake Chaya and Lake Bangweulu.

* To median rays of caudal fin.

The range of lengths for 19 specimens was from 24 to 61 cm., and four (34 to 43 cm.) weighed from 340 to 590 gm. Unfortunately it was impossible to weigh the largest fish, but they must have been about 2 to 2·5 kg. Much larger specimens, up to 16 kg., are said to have been caught in the Luapula River (Pitman, 1934, p. 317).

The gonads of many of the fish were examined, but almost all were undeveloped. One specimen of 59 cm. was a female with a ripe ovary.

This fish is a fierce predator and is important in the economy of the lakes and rivers, as it feeds on the smaller fish and helps to control their numbers. A large number of stomachs were examined; most were empty, but the rest contained fish remains.

In colour it is yellow with a series of longitudinal black stripes, and the caudal fin is usually bright red.

CITHARINIDAE.

DISTICHODUS MACULATUS Boulenger. 'Luwalwe', 'Lukase', 'Chika malunshi'.

There are 6 specimens from the Bangweulu Region in the British Museum, one collected by Melland and the rest by Pitman; 8 specimens (67+16 to 225+50 mm.) were collected from the Chambezi River, the Bangweulu Swamps and Lake Bangweulu: 4 (67 to 113 mm.) from station 209, one (225 mm.) from station 250, 2 (128 to 163 mm.) from station 266 and one (153 mm.) from station 268.

These fish are similar to those collected by Melland, and they all fit into Boulenger's description except that the interorbital width is rather narrow: eye $1\frac{1}{4}$ to $1\frac{2}{3}$ times in interorbital width (2 to $2\frac{1}{2}$ times). Worthington (1933 *b*, p. 39) pointed out that Pitman's specimens were also narrow in the interorbital; eye $1\frac{1}{2}$ to $1\frac{2}{3}$ times in the interorbital width. These fish were also rather deep in the body, depth $2\frac{2}{3}$ to $2\frac{4}{5}$ times in length, and the spots on the sides were very indistinct. The present specimens are about the usual depth, 3 to nearly $3\frac{1}{2}$ times in length (3 to $3\frac{1}{3}$ times), and the body is silvery grey with quite well marked dark spots. The colour is lighter underneath and the tips of the fins are pink.

Ecology. This fish is quite common in the Chambezi River, and large numbers of small specimens were taken in a fish poisoning near the Safwa Falls. Only very few large fish were seen, two of these were from the Chambezi, two from Matipa in the swamps and one from Muchinchi on Lake Bangweulu.

The range of lengths for 8 specimens was from 8 to 29 cm., and the 4 largest (20 to 29 cm.) were females with ripening ovaries; 4 stomachs were empty and one was filled with pieces of weed.

This fish is silvery grey in colour with dark spots on the sides.

NANNOCHARAX MINUTUS Worthington (1933 *b*, p. 40).

10 specimens in the British Museum collected by Pitman from a swamp near the Luombo River; 2 specimens (26+5 to 27+6 mm.) collected from the Bangweulu Swamps, station 266.

CYPRINIDAE.

BARILIUS NEAVII Boulenger. 'Kasonsomya'.

No *Barilius* previously recorded from this region, but there are specimens in the British Museum from a mountain stream near Petauke, Zambesi System.

Four specimens (54+14 to 103+ ? mm.) from the Mansya and Chambezi Rivers: the 3 largest from station 204 and the smallest from station 209.

These fish were mostly bought off small native boys and are badly damaged, but they appear to belong to this species, though they differ in having slightly shorter fins and a greater number of dark bars on the side of the body. They are also very similar to the closely related species *B. ubangensis* Pellegrin from South Cameroon and Upper Congo, and it may be that further material will show that the two species are merely local variations of one more widespread form.

BARBUS TRIMACULATUS Peters. 'Mushipa'.

25 specimens from the Bangweulu Region in the British Museum, collected by Pitman; 21 specimens (49+15 to 90+25 mm.) from the Chambezi River and the edge of Lake Bangweulu, 20 from station 252 and one large one from station 268.

These fish fit into the description, except that the dorsal spine is long and the caudal peduncle is sometimes rather deep: dorsal spine a little longer to 1¼ times as long as head (⅔ to once as long) and caudal peduncle 1½ to twice as long as deep (1⅔ to twice). The dorsal spines of some of Pitman's specimens are also longer than in the description, but they are not as long as in the new fish.

BARBUS PALUDINOSUS Peters.

There are 39 specimens from the Luombwa River in the British Museum, collected by Pitman; 6 specimens (37+13 to 69+21 mm.) collected from the Chambezi River and the edge of Lake Bangweulu: two (50 to 52 mm.) from station 252 and four (37 to 69 mm.) from station 268.

These fish are typical except that the dorsal spine is rather long, 1 to 1⅓ times as long as head (as long as or a little shorter than head, rarely a little longer) and longer than in Pitman's specimens of the same size. The specimens from Lake Rukwa also have rather long spines.

BARBUS EUTÆNIA Boulenger. 'Mushipa'.

One specimen from the Bangweulu Region in the British Museum collected by Pitman; 3 specimens (75+? to 122+? mm.) collected from the Mansya River, station 204.

These fish fit into the description.

BARBUS MULTILINEATUS Worthington (1933 *b*, p. 44). 'Bwelele' 'Kasenga' *.

18 specimens from near the Luombo River in the British Museum, collected by Pitman, and there are specimens at Tervueren from the Luombwa-Luapula confluence; 26 specimens (24+7 to 34+10 mm.) collected from the Bangweulu Swamps, station 266.

Many of these fish are larger than the type specimens, but they fit into the description except that the head is sometimes rather small: head 3½ to 4 times in length (3⅘ to 4 times).

BARBUS VERNAYI Nichols & Boulton (1927).

There are 56 specimens at Tervueren from the Luapula-Luombwa confluence, but none in the British Museum; 13 specimens (25+8 to 30+9 mm.) collected from the Bangweulu Swamps, station 266.

A new description of the species is given by David and Poll (1937, p. 217), and is based on specimens from 40 to 43 mm. The present specimens are, therefore, slightly smaller, and they differ from the description in the following respects: depth of body 3¾ to 4⅕ times in length (instead of 3 to 3½ times); dorsal spine 1 to 1⅓ times in length of head (1½ to 1⅘ times); caudal peduncle 2 to 2½ times as long as deep (almost twice); scales 28 to 32 along lateral line (29 to 32) and 12 to 14 round caudal peduncle (12).

BARBUS LORNÆ†, sp. nov.

Depth of body 3½ to 4 times in length, length of head 3⅔ to 4¼ times. Snout rounded, as long as or slightly shorter than eye, which is 3 to 3½ times in length of head; interorbital width 2¾ to 3 times in length of head; mouth small, terminal, 3 to 3½ times in length of head; two barbels on each side, anterior ¾ to once as long as eye, posterior 1¼ to 1¾ times. Dorsal III 7 (8 in one specimen), about equally

* These names seem to be applied to any small species of fish.
† The specific name is in honour of Mrs. Gore Brown.

distant from posterior border of eye and base of caudal, border straight ; last simple ray not enlarged or serrated, $\frac{3}{4}$ to as long as head. Anal III 5, not reaching caudal Pectoral $\frac{3}{4}$ to $\frac{5}{6}$ length of head, not reaching pelvic ; base of pelvic below dorsal. Caudal forked. Caudal peduncle $1\frac{2}{3}$ to twice as long as deep. Scales radiately striated, 26 to 28, $\frac{4\frac{1}{2}}{4\frac{1}{2}-5\frac{1}{2}}$, $2\frac{1}{2}$–3 between lateral line and pelvic, 12 round caudal peduncle ; lateral line complete. Dark above, yellowish beneath ; fins grey ; a series of black spots along the side of the body, connected by a dark lateral streak ; the spots may sometimes be rather indefinite in the streak, and all but the last two are above the lateral line.

This description is based on ten specimens (17+5 to 54+14 mm.) from Lake Young and the Mansya River : the largest from the Katete River, station 70, six (17 to 36 mm.) from the edge of Lake Young, stations 20, 22, 30, 31 and 43, and three (24 to 36 mm.) from the Mansya River, station 204.

This species comes near to *B. lineomaculatus* Boulenger from the East African rivers, but differs in having a rather larger eye, only seven branched rays in the dorsal fin and fewer scales along the lateral line. It is also very similar to *Barbus luluae* Fowler, but differs in having fewer dorsal rays, a thinner caudal peduncle and different markings.

Barbus banguelensis Boulenger.

There is one specimen from Lake Bangweulu in the British Museum, collected by Melland, and 20 from near the Luombwa River, collected by Pitman ; 13 specimens (45+16 to 81+21 mm.) collected from the Bangweulu Swamps, station 266.

These fish seem to be similar to Pitman's specimens except that they all have eight branched rays in the dorsal fin instead of seven to eight. Worthington (1933 *a*, p. 304) shows that specimens from Lake Nyasa all have eight rays.

Barbus unitaeniatus Günther. 'Bwelele', 'Mushipa'.

29 specimens from the Luombwa River and three from the Chambezi System in the British Museum, collected by Pitman ; 4 specimens (25+7 to 39+11 mm.) collected from the Chambezi River and the Bangweulu Swamps, the three smallest (25 to 29 mm.) from stations 209 and 252 and the largest from station 266. These fit into the description and are similar to Pitman's specimens.

There are also 21 (31+9 to 40+12 mm.) collected from the edge of Lake Bangweulu, station 268. These apparently belong to the species *B. unitaeniatus*, but differ from the other specimens in having a narrower interorbital width, a longer body and very few dark markings.

Barbus barilioides Boulenger.

This species had previously been recorded from the Luombwa River (David and Poll, 1937, p. 220), but the only specimens in the British Museum are the types from the Solwezi, Zambezi System, collected by Melland ; 12 specimens (24+8 to 37+12 mm.) collected from the Bangweulu Swamps, station 266.

These fish are typical.

Barbus brevidorsalis Boulenger (1915, p. 167 ; see ref. 1920).

30 specimens from near the Luombo River in the British Museum, collected by Pitman ; 14 specimens (19+4 to 33+8 mm.) from the edge of Lake Young, Shiwa Ngandu, stations 20, 22, 30, 31 and 43.

These fish are similar to Pitman's specimens, but they all differ from the description in having 7 instead of 6 branched rays in the dorsal fin.

Barbus lineomaculatus Boulenger.

There are specimens from the Luombwa River at Tervueren, but none from the Bangweulu Region in the British Museum or in the present collection.

BARBUS OWENAE *, sp. nov.

Depth of body 4 to 4½ times in length, length of head about 4 times. Snout rounded, shorter than eye, which is 2⅖ to just over 3 times in length of head; interorbital width 3 to 3½ times in length of head; mouth very small, terminal, about 4½ times in length of head; a single small barbel on each side, which is ⅓ to ⅖ diameter of eye. Dorsal III 8, equally distant from base of caudal and anterior border or centre of eye, border slightly concave; last simple ray not enlarged or serrated, once to 1⅙ times as long as head. Anal III 5, not reaching caudal. Pectoral ⅔ to ¾ length of head, not reaching pelvic; base of pelvic below dorsal. Caudal very deeply forked. Caudal peduncle 2½ to 3 times as long as deep. Scales radiately striated, 29 to 32 in longitudinal series, $\frac{4\frac{1}{2}}{3\frac{1}{2}-4\frac{1}{2}}$, 2 to 2½ between lateral line and pelvic, 12 round caudal peduncle; lateral line incomplete, with tubules only on anterior 5 to 10 scales. Silvery in colour, darker above; scales on the back with dark edges, and scales along lateral line series often dark at the base; a dark lateral streak sometimes with black spots; a black spot at the base of dorsal and anal fins; a dark streak along underside of caudal peduncle.

This description is based on 13 specimens (28+9 to 37+12 mm.) collected from the edge of Lake Bangweulu, station 268. The new species comes near to *B. rogersi* Boulenger from Angola, the Upper Zambesi and Lake Nyasa, but differs in having a longer, thinner body, an incomplete lateral line and a different scale formula.

BARBUS HAASEANUS David (1936, p. 73).

Four specimens have previously been collected from the Bangweulu Region, but there are none in the British Museum; 8 specimens (18+5 to 21+6 mm.) collected from the Bangweulu Swamps, station 266.

These fish seem to be typical, but the description must be enlarged in certain characters to include them: depth of body 3½ to 4 times in length (4 times), length of head 3½ to 3¾ times (3½ times); snout about ⅔ diameter of eye (shorter than eye), which is 2½ to 3 times in length of head (3 times); dorsal III 8 (II 8) and anal III 7 (II 7); scales 34 to 36 in longitudinal series (35 to 36), 14 round caudal peduncle.

BARBUS MACROTÆNIA Worthington (1933*a*, p. 305).

There is one small specimen at Tervueren from the Luombwa River which has been recorded as this species by David and Poll (1937, p. 222), but they are doubtful whether it is similar to the single type specimen from Lake Nyasa.

There are no ecological data for any of the *Barbus* because the species were not differentiated in the field.

LABEO ALTIVELIS Peters. 'Inanga', 'Pumbu'.

Eight specimens from the Bangweulu Region in the British Museum, four collected by Melland and four by Pitman; 3 specimens (185+? to 280+65 mm.) from the Chambezi River and Lake Chaya: one from each of the stations 209, 251 and 262.

These fish fit into the description except that the largest is too deep in the body and too wide in the interorbital: the measurements for these characters in the new specimens are: depth of body 2¾ to 3⅛ times in length (3 to 3¼ times) and interorbital width 1¾ to just over twice in length of head (2 to 2⅓ times).

Ecology. This fish is fairly common in the Chambezi River and Lake Chaya, but it was never seen in Lake Bangweulu or the Swamps.

The range of lengths for 11 specimens was from 18 to 33 cm., and the five largest (29 to 33 cm.) weighed from 300 to 400 gm.

* The specific name is in honour of Miss R. J. Owen.

The gonads of 6 large specimens were examined, but all were undeveloped except one fish of 28 cm. which had a ripe ovary; 5 stomachs were examined, but they were all empty.

In colour this fish is greenish on the back, paler underneath and has pink spots on the sides and pinkish fins.

LABEO SIMPSONI*, sp. nov. 'Lukunyu'.

Depth of body $4\frac{1}{4}$ to $4\frac{3}{4}$ times in length, length of head 4 to $4\frac{1}{2}$ times. Head $1\frac{1}{3}$ to $1\frac{1}{2}$ times as long as broad; snout rounded, strongly projecting beyond mouth, longer than postocular part of head; eye supero-lateral, in second half of head, $5\frac{1}{2}$ to $6\frac{3}{4}$ times in length of head, $2\frac{1}{2}$ to 3 times in interorbital width; width of mouth $1\frac{3}{4}$ to twice in length of head; rostral flap and posterior border of lip feebly denticulated; inner surface of lips with numerous feeble transverse plicae; a small barbel hidden in folds of skin; snout with numerous tubercles. Dorsal II 10, equally distant from end of snout and base of caudal; the last simple and anterior branched rays greatly prolonged, $1\frac{3}{5}$ to twice as long as head. Anal II 5; longest ray $\frac{3}{4}$ to nearly once length of head. Pectoral $\frac{7}{8}$ to a little longer than head, not reaching pelvic, the 1st ray of which falls under 5th branched ray of dorsal. Caudal deeply forked. Caudal peduncle $1\frac{1}{3}$ to $1\frac{1}{4}$ times as long as deep. Scales 34, $\frac{4\frac{1}{2}}{6\frac{1}{2}}$, 3 between lateral line and root of pelvic, 12 round caudal peduncle. Dark grey above, whitish beneath, with rather indistinct dark lateral band; edges of scales dark; fins grey.

This description is based on two specimens (134+40 to 250+68 mm.) from the Chambezi River, station 209. A third specimen (86 mm.) was also taken at this station.

This species is very near to *L. annectens* Boulenger, from Cameroon, Ogowe and Upper and Lower Congo River, but differs in having a longer head and very long rays in the dorsal fin. In the prolongation of the dorsal rays the new specimens resemble the closely related species *L. chariensis* Pellegrin from Cameroon, Gold Coast and Lower Congo River, and this is the main distinguishing character between *L. chariensis* and *L. annectens*. In some species of *Labeo*, notably *L. forskalii* Rüppell and *L. percivali* Boulenger, the long dorsal rays have been shown to be a secondary character found only in adult males. If further work shows that in many species the dorsal fins of the males do become prolonged, it may be necessary to reorganize some of the species that have been separated on this character. Until further material is forthcoming, however, it is thought best to consider the specimens from the Chambezi River as a separate species.

LABEO DARLINGI Boulenger.

There is one specimen at Tervueren from the Luombwa River, but it differs slightly from the original description based on specimens from the Zambesi and Limpopo Rivers. This specimen is very similar to those described above, and it is possible that when it is possible to examine the Luombwa specimen, it will be found to belong to the new species.

BAGRIDAE.

AUCHENOGLANIS OCCIDENTALIS (Cuvier & Valenciennes). 'Mbowa', 'Mboko-boko'.

One specimen from Lake Bangweulu in the British Museum, collected by Melland; 7 specimens (32+8 to 335+60 mm.) collected from the Chambezi River, Lake Chaya and Lake Bangweulu; one (83 mm.) from station 209, one (105 mm.) from station 250, one (335 mm.) from station 251, one (285 mm.) from station 262 and three (32 to 128 mm.) from station 268.

These all fit into the description.

* The specific name is in honour of the late Mr. Charles Simpson.

Ecology.—These fish are common in the more open water, and a few were seen in the swamps. It is said to be abundant in the open part of Lake Bangweulu, where it is fished by the natives on a large scale.

The range of lengths for 7 specimens was from 4 to 54 cm., and the largest was a male with a developing gonad.

One stomach was examined and was empty.

This fish is usually grey in colour, with large round dark spots on the sides and fins.

CHRYSICHTHYS MABUSI Boulenger. 'Chiminanjiri', 'Mafusa'.

A single specimen from Lake Bangweulu in the British Museum, collected by Melland; 4 specimens (38+10 to 275+70 mm.) from the Chambezi River and Lake Chaya: the smallest from station 209, one (250 mm.) from station 212, one (260 mm.) from station 252, and one (275 mm.) from station 262.

These are similar to Melland's fish, but the description, which is based on a single specimen (220+50 mm.), must be enlarged as follows to include the new specimens: length of head 3 to $3\frac{1}{3}$ times in length of body (3 times); eye $5\frac{1}{2}$ to 6 times in length of head (6 times), 2 to $2\frac{1}{2}$ times in interorbital width ($2\frac{1}{2}$ times); nasal barbel a little shorter to $1\frac{1}{2}$ times as long as eye (shorter), maxillary barbel $\frac{1}{2}$ to $\frac{5}{7}$ length of head ($\frac{1}{2}$), and outer mandibular barbel $\frac{2}{5}$ to $\frac{1}{2}$ length of head ($\frac{2}{5}$); gill rakers 14 to 16 (16); dorsal spine $1\frac{2}{3}$ to twice in length of head ($1\frac{1}{2}$ times), longest soft ray $1\frac{1}{3}$ times (a little shorter than head); anal II-III 7-8 (II 7); caudal peduncle $1\frac{1}{2}$ times as long as deep ($1\frac{2}{3}$ times).

Ecology.—Only a few of these fish were seen, but it is probably common in the more open water. Specimens were caught in the Chambezi River and Lake Chaya, and several large ones were seen from the open part of Lake Bangweulu.

The range of lengths for 8 specimens was from 5 to 56 cm., and one (50 cm.) was a female with a ripening ovary.

Three stomachs were examined: one was empty, one contained fish remains and one was filled with 12 snail shells.

This fish is greenish in colour.

SCHILBEIDAE.

EUTROPIUS BANGUELENSIS Boulenger. 'Lupata'.

A single specimen in the British Museum from Lake Bangweulu, collected by Melland: 1 specimen (220+55 mm.) collected from Lake Chaya, station 262.

This fish fits into the description except that all the barbels are a little long.

SCHILBE MYSTUS (Linnaeus). 'Lupata'.

17 specimens from the Bangweulu Region in the British Museum, one collected by Melland and the rest by Pitman; 3 specimens (100+? to 195+29 mm.) collected from the Chambezi River and the Bangweulu Swamps: the smallest from station 209, the largest from station 250, and the third (185 mm.) from station 265.

These are all typical.

Ecology.—This species is common in the more open waters and was caught in the Chambezi River, Lake Chaya, in channels in the swamps near Matipa and in the open part of Lake Bangweulu off Muchinchi.

The range of lengths for 15 specimens was from 12 to 37 cm., and the four largest (28 to 37 cm.) weighed from 170 to 310 gm.

There are no data about breeding.

This fish is a predator. Most of the stomachs examined were empty, but three contained remains of fish, including pieces of an *Alestes*.

In colour it is a pale silvery grey.

CLARIIDAE.

HETEROBRANCHUS LONGIFILIS * Cuvier & Valenciennes. 'Sampa' 'Sapika'.

Not previously recorded from the Bangweulu Region.

One specimen (220+35 mm.) from near the Chambezi-Mansya confluence, station 207.

This fish fits into the description.

CLARIAS GARIEPINUS (Burchell). 'Moota', 'Milonge', 'Kapola'.

10 specimens from the Bangweulu Region in the British Museum, two collected by Melland and the rest by Pitman; 2 specimens (215+50 to 350+52 mm.) collected from the Chambezi River: the smaller from station 207 and the larger from station 250.

These specimens fit into the description.

Ecology.—This species was not distinguished from *C. mellandi* in the field, and it may have been present also in the swamps and in Lake Bangweulu.

CLARIAS MOSSAMBICUS Peters.

Two specimens from the Bangweulu Region in the British Museum, one collected by Melland and one by Pitman.

Not represented in the present collection.

CLARIAS MELLANDI Boulenger. 'Moota'.

Four specimens from the Bangweulu Region in the British Museum, two collected by Melland and two by Pitman; 2 specimens (285+45 to 300+55 mm.) from the Bangweulu Swamps, station 263.

These fish are typical except that the larger is rather long in the body, has too few fin rays and a long caudal fin, as shown by the following: depth of body $6\frac{1}{2}$ times in length ($5\frac{1}{2}$ times); dorsal rays 55 (65) and anal rays 50 (55) in number; caudal fin $\frac{5}{8}$ length of head ($\frac{1}{2}$).

Ecology. Both specimens were females with ripening or ripe ovaries.

'Moota' (*C. gariepinus* or *C. mellandi*) are said to be abundant all over the swamps, where they are caught in large numbers by the natives.

CLARIAS STAPPERSII Boulenger (1915, p. 168; *see* ref. 1920). 'Chineke'.

Two specimens from the Bangweulu Region in the British Museum, collected by Pitman; a single specimen (240+25 mm.) collected from the Chilola–Chambezi confluence, station 252.

This fish is rather shrivelled and difficult to identify, but it appears to be similar to Pitman's specimens. As pointed out by Worthington (1933 *b*, p. 48), these fish differ considerably from Boulenger's description, but they nearly fit into the newer description given by David (1935, tab. 5). It has not been possible to see the type and compare it with the specimens from the Bangweulu Region.

CLARIAS YOUNGICUS, sp. nov. 'Milonge'.

Depth of body $6\frac{1}{3}$ to 7 times in length, length of head 4 to $4\frac{1}{3}$ times. Head $1\frac{1}{3}$ to $1\frac{2}{5}$ times as long as broad, smooth; occipital process broadly pointed, angle acute; frontal fontanelle knife-shaped, 4 to 5 times in length of head; occipital fontanelle smaller, not or slightly encroaching on occipital process; eye very small, 3 to 4 times in snout and $6\frac{1}{2}$ to $7\frac{1}{2}$ times in interorbital width, which is equal to the width of mouth and 2 to $2\frac{1}{3}$ times in length of head; band of praemaxillary teeth $3\frac{1}{2}$ to $4\frac{1}{2}$ times as long as broad; vomerine teeth forming a curved band which is a

* It seems probable that the fish from the Loangwa Valley, collected by Pitman and described as a new species, *Clarias loangwensis*, by Worthington (1933 *b*, p. 46), may really be a *Heterobranchus*. The caudal region of the specimen has been damaged and partly regenerated, so that the adipose fin, one main distinguishing character of the two genera, may have disappeared. In all characters, apart from those connected with the caudal region, this fish appears to be identical to *H. longifilis*.

little narrower than or equal in width to the praemaxillary band; nasal barbel $\frac{1}{2}$ to $\frac{3}{5}$ length of head, maxillary barbel $\frac{3}{4}$ to $\frac{7}{8}$, outer mandibular barbel $\frac{2}{3}$ to $\frac{3}{4}$, and inner mandibular barbel $\frac{1}{2}$ to $\frac{2}{3}$. Gill rakers few, 8 to 9 on anterior arch. Clavicles concealed under the skin. Dorsal 68 to 75, its distance from occipital process $\frac{4}{5}$ to $\frac{1}{2}$ length of head and its distance from caudal equal to once or twice diameter of eye. Anal 52 to 58, also separated from caudal. Pectoral $\frac{3}{7}$ to $\frac{1}{2}$ length of head, the spine feebly serrated on outer side and $\frac{2}{3}$ the length of fin. Pelvic $1\frac{1}{4}$ to $1\frac{1}{3}$ times as distant from caudal as from end of snout. Caudal $\frac{4}{9}$ to $\frac{1}{2}$ length of head. Dark brown above, lighter beneath; a light, dark-edged curved band on the caudal; light edge to dorsal fin; anal fin lighter than dorsal.

This description is based on 6 specimens (190+22 to 260+28 mm.) collected from Lake Young, Shiwa Ngandu: three (190 to 210 mm.) from station 11 and three (200 to 260 mm.) from station 23.

This species is near *C. stappersii*, but differs in having longer barbels and a shorter and broader head. According to David's classification (1935) it would come between *C. submarginatus* Peters and *C. carsonii* Boulenger, and, like *C. stappersii*, would probably be considered as a "weitere Lokalform" of *C. submarginatus*.

Ecology. This fish is quite common in Lake Young, and 18 specimens were taken in gill-nets at various stations round the edge of the lake.

The range of lengths for 18 specimens was from 21 to 34 cm. There were six females (22 to 34 cm.) and one male with developing gonads, while the rest were quiet.

Fifteen stomachs were examined: six were empty, five contained remains of fish only, two contained fish and weed, one contained a large tadpole (6 cm. in length), and in one the contents were unrecognizable.

CLARIAS BYTHIPOGON Sauvage.

Not previously recorded from the Bangweulu Region, but there are specimens from the Upper Congo in the British Museum. One specimen (67+9 mm.) collected from the edge of Lake Bangweulu, station 268.

This fish is difficult to identify as it is so small, but it appears to fit into the description except that it has too few gill rakers, 12 (instead of 17 to 22), but this may be a character of young specimens.

CLARIAS THEODORAE Weber. 'Mulonfi'.

18 specimens from the Bangweulu Region in the British Museum, collected by Pitman; 16 specimens (45+6 to 150+15 mm.) collected from the Bangweulu Swamps and from the edge of Lake Bangweulu: 11 (45 to 92 mm.) from station 266 and 5 (100 to 150 mm.) from station 268.

There is also a very small specimen (27+3 mm.) from Lake Young, station 86, which probably belongs to this species, but it is too small to identify with certainty.

One specimen (11 cm.) had a ripe ovary.

MOCHOCHIDAE.

SYNODONTIS NIGROMACULATUS Boulenger, 1905. 'Chinyimba', 'Konkonko'.

There are two specimens from Lake Bangweulu in the British Museum, collected by Melland, but one of these has been named *S. melanostictus* Boulenger; 10 specimens (77+23 to 220+70 mm.) collected from the Chambezi River, the Bangweulu Swamps and Lake Bangweulu: one (125 mm.) from station 209, two (77 mm.) from station 252, two (150 to 165 mm.) from station 265, two (140 to 150 mm.) from station 266 and three (175 to 220 mm.) from station 271.

These fish all fit into the description.

The species *S. nigromaculatus* was described from a single specimen from Lake Bangweulu. According to the description it differs from *S. melanostictus* (described in 1906) in having smooth, instead of villose, skin on the sides and large black spots often

confluent into vermicular lines, instead of small separate black spots. The dorsal spine also tends to be shorter and the humeral process narrower. The new material, however, shows that the villosities are probably not a good character for separation as they depend on the state of preservation of the fish, that there is every variation in the markings, both in the size of the spots and the extent to which they are joined into lines, and that the length of the dorsal spine and width of humeral process are variable. When the characters of the new specimens had been tabulated and compared with those of the fish already in the British Museum, no significant differences could be found, and it is thought best to unite the two species under the older name, *S. nigromaculatus*.

Ecology.—This fish was seen in most of the Bangweulu Region, but it seems to be most common in the Chambezi River and Lake Bangweulu, and off Muchinchi 10 fish were taken in a single 2-inch mesh gill-net.

The range of lengths for 20 specimens was from 10 to 30 cm., and one female (27 cm.) with a ripe ovary weighed 200 gm.

There are no data about feeding habits.

SYNODONTIS ORNATIPINNIS Boulenger. 'Konkonko'.

A single small specimen (98+ ? mm.) was collected from the Chambezi River, station 209.

It is similar to *S. ornatipinnis* from the Congo, Lake Mweru, and the Luombwa River, but differs from the description in having a smaller head, a smaller eye and fewer and more distinct black bands on the dorsal, pelvic, anal and caudal fins. With further material it will probably be necessary to separate this fish from *S. ornatipinnis*, but at present, with only a single small specimen, I am loth to make a new species.

EUCHILICHTHYS GUENTHERI (Schilthuis). 'Kolokota'.

This species had not previously been recorded from the Bangweulu Region. One specimen (210+50 mm.) collected from the Chambezi River, station 209.

This fish fits into the description except that the interorbital width is rather narrow and the dorsal and pectoral spines are a little long: eye $4\frac{1}{2}$ times in interorbital width (5 times); dorsal spine $2\frac{1}{2}$ times in length of head (3 times) and pectoral spine $1\frac{1}{2}$ times ($1\frac{2}{3}$ times).

CYPRINODONTIDAE.

APLOCHEILICHTHYS MOERUENSIS (Boulenger).

Three specimens from the Luombo River in the British Museum, collected by Pitman. There are specimens from the Luombwa River at Tervueren. About 250 specimens (12+4 to 33+8 mm.) collected from Lake Young, the Chambezi River and the Bangweulu Swamps: 70 (12 to 30 mm.) from stations 13, 14, 19, 22, 25, 32 and 42; 4 (20 to 31 mm.) from station 209, 131 (19 to 33 mm.) from station 252 and 49 (21 to 30 mm.) from station 266. There are also many small specimens, too small to identify, from station 86.

These fish probably all belong to this species, but there is great variation among the specimens. The main differences from the description are that the depth of the body may be over 5 times in the length ($4\frac{1}{3}$ to $4\frac{1}{2}$ times), there may be 9 rays in the dorsal fin (7–8), the caudal peduncle may be only $1\frac{1}{2}$ times as long as deep (twice), and there may be 29 scales in a horizontal series along the body (26–28). The specimens from Lake Young appear to be less variable than the others, to be deeper in the body and a larger proportion have 9 rays in the dorsal fin. Worthington (1933 *b*, p. 50) shows that Pitman's specimens also differ from the description in certain characters, and it may be necessary in the future to consider the Rhodesian fish as distinct from those from Lake Mweru.

APLOCHEILICHTHYS KATANGAE (Boulenger).

There are 7 specimens from the Chambezi System in the British Museum, collected by Pitman. There are specimens from the Luombwa River at Tervueren ; five specimens (17+5 to 21+5 mm.) collected from the Bangweulu Swamps, station 266. There are also five very small specimens from station 252.

These fish are deeper in the body than those of the previous species and appear to be similar to Pitman's specimens, but they all differ in several characters from the description (see Worthington, 1933 *b*, p. 51). Further work is needed on these two species of *Aplocheilichthys*.

CICHLIDAE.

TYLOCHROMIS BANGWELENSIS Regan (1920 *b*, p. 167. 'Kwempe', Tembwe', 'Nsangula'.

11 specimens from the Bangweulu Region in the British Museum, four collected by Melland and the rest by Pitman ; 8 specimens (80+20 to 190+50 mm.) collected from the Chambezi River, the Bangweulu Swamps and Lake Bangweulu, one from each of the following stations : 209, 251, 266 and 268 (150, 175, 150 and 190 mm. respectively), and 4 (80 to 100 mm.) from station 268.

These fish fit into the description.

Ecology. This species is not very abundant, though several were taken at the edge of Lake Bangweulu.

The range of lengths for 9 specimens was from 10 to 25 cm. Two fish (18 to 22 cm.) were breeding, one was a female with a ripening ovary and the larger was a male with a ripe testis.

There are no data about feeding habits.

This fish is generally light yellowish green in colour, often with red on the head, the front of the body, the pelvic and the lower lobe of the caudal fin.

TILAPIA MACROCHIR Boulenger. 'Nkamba', 'Mtuuba', 'Isama'.

Nine specimens from the Bangweulu Region in the British Museum, seven collected by Melland and two by Pitman ; 6 specimens (80+25 to 190+50 mm.) collected from the Chambezi River, the Bangweulu Swamps and the edge of Lake Bangweulu : one (160 mm.) from station 250, one (190 mm.) from station 263 and four (80 to 110 mm.) from station 268.

These fish all fit into the description.

Ecology. Only one specimen was seen in the Chambezi River, while four were taken in the swamps, five from the edge of Lake Bangweulu and two large ones were caught in a 5-inch mesh gill-net set out in the open water.

The range of lengths for 12 specimens was from 11 to 31 cm., and the weights of five (20 to 31 cm.) were from 170 to 660 gm. The three largest fish were breeding : one of 29 cm. and 540 gm. was a male with a ripe testis, one, of 30 cm. and 570 gm., was a female with an ovary starting to develop, and the third, of 30 cm. and 600 gm., had its gonad spent.

Four stomachs were examined : one from the open water was empty, but the other three, from the swamps, contained pieces of weed, algae, zooplankton and a few small fish-bones.

In colour this fish is rather pale grey, and is sometimes striped with dark red.

TILAPIA MELANOPLEURA Dum. 'Pende'.

14 specimens from the Bangweulu Region in the British Museum, six collected by Melland and eight by Pitman ; 4 specimens (75+20 to 210+60 mm.) from the Chambezi, the Bangweulu Swamps and the edge of Lake Bangweulu : two (180 to 210 mm.) from station 250, one (135 mm.) from station 266 and one (75 mm.) from station 268.

These fish all fit into the description.

Ecology. Only one specimen was seen in Lake Bangweulu, but it was very common in the Chambezi River and in the swamps.

The range of length for 9 fish was from 9 to 30 cm. The gonads of 5 specimens were examined: two fish of 17 and 25 cm. had undeveloped gonads, one of 26 cm. was a female with a ripening ovary and the two largest, of 28 and 29 cm. and 400 and 500 gm., were males with their gonads spent.

Two stomachs were examined and found to contain pieces of weed and general vegetable debris, showing that the fish were feeding among the weeds.

This fish is dark green in colour on the back and is often pink underneath.

TILAPIA SPARRMANII Smith. 'Ntuku', 'Katanga'.

31 specimens in the British Museum from the Bangweulu Region, 6 collected by Melland from Lake Bangweulu and the rest collected by Pitman, 9 from the Luombo River, 12 from the Lukulu River and 4 from Lake Young; 64 specimens were collected from Lake Young, the Mansya and Chambezi Rivers, the swamps and the edge of Lake Bangweulu: 30 (95+25 to 185+45 mm.) from stations 2, 3, 7, 11, 12, 16,1 7, 23, 32, 34, 38, 80; 3 (92+28 to 100+30 mm.) from stations 207 and 208; 1 (42+13 mm.) from station 209: 4 (100+30 to 110+35 mm.) and 25 (22+8 to 55+17 mm.) from stations 263 and 266; and 1 (70+20 mm.) from station 268.

The fish from Lake Young differ slightly from those caught in the Chambezi River or Lake Bangweulu in having rather wider mouths, narrower bodies and a tendency to a steeper profile. Some grew to a length of 230 mm., which is a very large size for this species.

Ecology. This fish was very abundant in Lake Young and the Mansya River, and it was also seen in small numbers all through the swamps and at the edge of Lake Bangweulu.

The size, feeding and breeding habits of the specimens from Lake Young are considered separately. Among 33 from the Mansya River, Chambezi River, swamps and Bangweulu, the range of size was from 5 to 15 cm. The two largest were males with ripe testes.

About 1,000 specimens were caught in Lake Young, and these were nearly all taken round the edge of the lake. The range of length was from 8 to 24 cm., and the range of weight for 181 specimens was from 30 to 250 gm. From the end of July till the middle of October, fish over 16 cm. were rarely taken, but after the middle of November and until we left the lake in mid-January, fish over 16 cm. were more commonly caught than smaller sizes. This was well shown by the effectiveness of different sized nets. During the first period over ten times as many specimens (ranging in length from 12 to 16 cm.) were taken in gill-nets of 2-inch mesh as in those of 3-inch mesh, but after November the 3-inch made the bigger catches.

Many gonads were examined. During the first period the great majority of the fish were not breeding, though a small proportion of the gonads were starting to develop. After November every specimen examined, both large and small, was breeding and many of the gonads were already spent. It was clear that the breeding season had started between September and the middle of November. Unfortunately we were on Lake Rukwa during this time, so that it is impossible to give details about the beginning of the season.

There is a considerable change of habits during the breeding season. Before breeding started, larger fish were rare near the edge of the lake. Although small ones could be taken in large numbers, particularly near river mouths, they were rarely seen in the water. After November, however, enormous numbers of fish could be seen in the shallow water near the shores, and wherever there was a sandy bottom the fish were building or guarding their nests. The nests were hollows in the sand, usually about 18 inches across, but varying with the size of the fish. The

nests of the smaller specimens were in very shallow water, often not more than 1½ to 2 feet in depth, and the larger fish were in rather deeper water and could be seen up to about 2 metres. The area of sand in the lake was extremely limited, so that the nests were crowded closely together, usually nearly touching each other.

The fish could sometimes be seen hollowing out the nests by swimming round with their heads in the sand. At the bottom of each nest there were a number of small holes, usually filled with a bunch of greenish eggs. The eggs were strictly guarded by one, or both, of the parents, which could be seen hovering over the nest. The guards were clearly very alert, and as soon as another fish approached they darted out and drove the intruder away. Since the nests were so closely packed that it was impossible for any fish to move far without approaching a neighbouring nest, the guarding fish were in a permanent state of excitement, hovering for a few seconds and then darting out in pursuit in one direction, hovering again and then darting out again.

No small fry were seen in the nests, and they were never seen in the mouths of their parents. Large numbers of fry were seen swimming at the extreme edge of the lake.

During the breeding season there is a change of colour, particularly among the males. The usual colour is a dark green, often reddish on the sides, with a series of dark vertical bars in the young. When breeding starts, the fish become very much darker in colour, some being almost black on the belly. The stripes are more marked, bright iridescent patches of green appear on the sides of the head and orange tips to the fins.

Many stomachs were examined. Most were filled with phytoplankton and pieces of weed, but four contained remains of small fish or fish-bones.

HAPLOCHROMIS PHILANDER (Weber). 'Sosolwe', 'Chikundwa'.

83 specimens in the British Museum: 5 collected by Melland from Lake Bangweulu and 78 collected by Pitman, 66 from Chinsali, 9 from the Lukulu River and 5 from the Luombo River; specimens at Tervueren from the Luombwa River are recorded as *H. moffati* Castelnau; 78 specimens collected from Lake Young, the Mansya River, the swamps and edge of Lake Bangweulu and Lake Chila (near Abercorn): 11 (20+5 to 65+15 mm.) from stations 30, 32, 33; 2 (60+15 to 75+20 mm.) from station 202; 52 (20+5 to 65+15 mm.) from station 266; 2 (33+7 to 42+8 mm.) from station 268; and 11 (20+4 to 64+18 mm.) from station 402.

Most of these fish fit into the description of *H. philander dispersus* Trewavas (1936, p. 73), but the specimens collected from Lake Young show a longer head and a larger mouth set more horizontally than in the type specimens. In these characters they resemble the subspecies *H. philander philander*, which is so far known only from the coastal ranges of Natal and Mozambique.

There are no ecological data for this species, except that they are often brightly coloured.

SERRANOCHROMIS ANGUSTICEPS (Boulenger).

There are specimens from the Luombwa River at Tervueren, but it seems probable that when these can be compared to the rest of the specimens from the Bangweulu Region it will be found that they also belong to the separate species *S. kafuensis* (see below).

SERRANOCHROMIS KAFUENSIS (Boulenger). 'Polwe'.

16 specimens from the Bangweulu Region in the British Museum, 6 collected by Melland from Lake Bangweulu and the rest by Pitman, 6 from the Chambezi and 4 from the Luombo Rivers; 5 specimens (145+35 to 240+50 mm.) collected from Chambezi River and the Bangweulu Swamps: two (145 to 155 mm.) from stations 207 and 209; one (240 mm.) from station 250; one (155 mm.) from station 263; and one (210 mm.) from station 264.

This species was originally described by Boulenger (1908, p. 494) as *Paratilapia kafuensis*, the type being a specimen (190+45 mm.) from the Kafue River collected by Codrington (this specimen is in the British Museum). Later Boulenger amalgamated this species with *P. angusticeps*, and this name was kept for the species, which Regan (1920 *a*, p. 45) transferred to the genus *Serranochromis*. On re-examination of the specimens in the British Museum it was decided that *S. kafuensis* was distinct from *S. angusticeps* and that all new specimens belonged to the former species. It is also suggested that among the British Museum specimens of *S. angusticeps*, three (90 to 100 mm.) collected by Ansorge from Mossamedes, one (130 mm.) from the Upper Zambezi collected by Vaughan Jones and five (140 to 220 mm.) from Lake Ngami collected by Woosnam should also be considered as *S. kafuensis*. The fish from Lake Ngami, however, differ slightly in having a rather smaller eye, a less concave profile and a slightly thicker caudal peduncle.

The original description of the specimen from the Kafue River has been enlarged in certain respects to bring it into line with the recent descriptions of the closely related species. The following are additional measurements of the same specimen :— depth of praeorbital bone $4\frac{2}{3}$ times in length of head, interorbital width $5\frac{1}{3}$ times, length of lower jaw nearly twice ; gill rakers sometimes bifid ; teeth conical and very small ; pharyngeal teeth slender, 11 in series along median line of lower pharyngeal, which is narrower than in *S. angusticeps* and diminishes towards the anterior more rapidly ; pelvic fin does not reach origin of anal.

Ecology.—This fish was fairly common in the Chambezi River and in the swamps.

The range of length for 8 specimens was from 18 to 30 cm. Two of 27 and 28 cm. weighed 200 and 280 gm. respectively, the smaller was ' spent ' and the larger was a male with a ripe testis. The gonads of three other fish were examined, two of 19 cm. were a female and a male starting, and one of 26 cm. was a female with a ripening ovary.

This fish is clearly a predator. Although two out of the three stomachs examined were empty, the third contained a small fish and the large mouth and short intestine indicate that it is carnivorous.

In colour it is green on the back, pale underneath and usually has large numbers of small red spots on the under part of the head and dark spots on the dorsal, anal and caudal fins.

SERRANOCHROMIS THUMBERGI (Castelnau). 'Nsuku", "Lufunka', 'Muliba', 'Ntasa'.

36 specimens in the British Museum, 10 collected by Melland from Lake Bangweulu and the rest collected by Pitman, 3 from the Chambezi River and 23 from the Lukulu River ; 10 specimens (17+3 to 220+60 mm.) collected from the Mansya and Chambezi Rivers and the Bangweulu Swamps : one (155 mm.) from station 207 ; one (90 mm.) from station 209 ; two (200 to 220 mm.) from stations 250 and 251 ; one (230 mm.) from station 263 ; two (195 mm.) from station 264 ; one (220 mm.) and two (15 to 25 mm.) from station 266.

These fish all fit into the description.

Ecology.—This fish was common in the Chambezi River and the swamps, but none were seen in the open lake.

The range of length of 13 specimens was from 2 to 42 cm. The three largest, of 30, 33 and 41 cm. and 400, 500 and 1,000 gm. respectively were males with testes, either ' ripening ' or ' starting '. Four fish from 19 to 28 cm. were females with ovaries ' ripe ', ' ripening ' or ' starting '. All the specimens (seven in number) examined were therefore breeding or preparing to breed.

Four stomachs were examined, but all were empty. The large mouth and short intestine suggest that this species is also predacious.

In colour it is dark bluish green on the back and pale, sometimes yellow, underneath.

SARGOCHROMIS MELLANDI (Boulenger). 'Mbidia', 'Lubidia', 'Sosolwe'.

Three specimens in the British Museum from Lake Bangweulu, collected by Melland and Foulon, and there are specimens at Tervueren from the Luombwa River; 14 specimens (21+4 to 160+40 mm.) collected from the Chambezi River and Lake Bangweulu: one (60 mm.) from station 209; one (160 mm.) from station 250; 3 (135 to 155 mm.) from station 263; 8 (21 to 150 mm.) from station 266; and one (55 mm.) from station 268.

These fish all fit into the description.

Ecology.—It was seen in small numbers in the Chambezi River, the swamps and in Lake Bangweulu. There are no data on feeding and breeding habits, except that one male of 20 cm. had a testis starting to develop, and that the intestines of these fish are long and green, suggesting that they feed on vegetable material.

ANABANTIDAE.

CTENOPOMA MULTISPINIS Peters. 'Nkomo'.

37 specimens in the British Museum from the Bangweulu Region, 4 collected by Melland from Lake Bangweulu and 33 collected by Pitman from the Luombwa River; 7 specimens (58+14 to 120+25 mm.) collected from the Chambezi River and the Bangweulu Swamps: three (58 to 60 mm.) from station 211; two (67 to 90 mm.) from station 252; and two (100 to 120 mm.) from station 272.

These fish fit into the description except that the two largest are rather long and thin; depth of body 4 to 4½ times in length (instead of 3½ to 4 times) and length of head 3⅜ to 3¾ times in length (3½ to 3⅜ times), and in one of the smaller fish there are 19 spines in the dorsal fin (17 to 18).

There are no ecological data except that this fish is able to leave the water and move short distances over dry ground. The two largest specimens collected in the swamps were both found on a footpath several yards from the nearest pool of water. The ground was still wet from a recent rainstorm and the natives believed that the fish had come down in the rain from the large river that runs across the sky.

CTENOPOMA NANUM Günther.

There are 8 specimens from the Luombwa River at Tervueren recorded as this species, but it seems unlikely that there are three species of *Ctenopoma* in this river (see next species).

Species.	Denticulation of gill cover.	Anal spines.	Length of pelvic fin.
C. nanum.....	2–5* / 1–2	VII–IX.	Not reaching anal, but produced into a filament extending beyond anal.
C. ctenotis.....	8–10 / 5–6	X	Not reaching anal.
Present and Pitman's specimens	8–10 / 5–6	VII–IX.	Not reaching anal, but produced into a filament.

* One specimen collected by Christy from Madjo, Ituri, had ¾ spines on one side of its head and ¼ on the other.

CTENOPOMA CTENOTIS (Boulenger) 1919, p. 403. 'Nkomo'.

Four specimens in the British Museum from the Luombwa River, collected by Pitman. The types of this species are from a ditch near the Lukuga River in Tanganyika and are in the British Museum; 6 specimens (32+8 to 45+13 mm.) from the Bangweulu Swamps, station 266.

This species is extremely closely related to *C. nanum* Günther from the Cameroon (types from Gaboon) and Congo System, but it is said to differ in the denticulation

of the gill cover, the number of anal spines and the length of the pelvic fins. In all other characters the description of *C. nanum* covers the description of *C. ctenotis*.

The present specimens have been named *C. ctenotis* because they fit best into the distribution range of that species, and as they are identical with Pitman's specimens. All these fish, however, have some characters of each of the two species, as shown in the table (see p. 215).

Of these characters, the spines on the gill cover may not be a good character (see footnote), and the length of the pelvic fin appears to be variable in specimens of the same size in the same locality, and may be only a sexual character.

The present specimens are all small, but it seems probable that when further material from this region is collected it will show that the two species must be united.

There are no ecological data.

MASTACEMBELIDAE.

MASTACEMBELUS SIGNATUS Boulenger. 'Muchiri'.

One specimen in the British Museum from Lake Bangweulu collected by Melland (275 mm., type). One specimen (160+5 mm.) collected from the Chambezi River, station 209.

This fish differs from the type in the following ways: depth of body 9¾ times in the length (instead of 10½ times), length of head 6½ times in length (7 times); the distance of the vent from the head 2⅛ times the length of the latter (2⅝ times); number of dorsal spines XXVII (XXIX); distance between first dorsal spine and head 3½ times in length of latter (4 times); the X-shaped dark markings on the sides are fewer in number and more indeterminate in shape.

There are no ecological data for this species.

SUMMARY.

The main waters in the Bangweulu Region are Lake Bangweulu and its swamps, the Chambezi River System and the Luapula River above the Mumbatuta Falls. The region is drained by the Luapula River and is the source of the Congo River.

Mr. Melland was the first to collect fish in the Bangweulu Region. Later collections have been made by Belgian naturalists, by Captain Pitman and, in 1936, by our expedition.

Sixty-seven species have now been recorded. Among these, six are endemic and three are doubtful records. The majority of the remaining species are found in some part of the rest of the Congo System. Not all of these have been recorded from the Luapula River, suggesting that there may formerly have been other connections between the Bangweulu Region and the Congo. The presence in the Bangweulu Region of a large number of fish known from the Zambezi suggests water connections between the Congo and Zambezi Systems, and the evidence from the fish fauna indicates that the main connection was probably between the upper tributaries of the Zambezi and those of the Luapula below the Mumbatuta Falls.

Most of the species are widespread within the Bangweulu Region, but the Luombwa River contains six fish not found elsewhere, and the fauna of Lake Young is effectively separated from the Chambezi River by the falls on the effluent river.

In studying the ecology of the fish, the fauna of the swamps, the open waters and Lake Young are considered separately. In the swamps there are few species, but large numbers of individuals, the commonest being cichlids and mormyrids. In the open water the fauna is more varied and there are more elaborate food chains. In Lake Young only three species are common. There are few data about breeding habits except in Lake Young, where the *Tilapia sparrmanii* were seen guarding their nests during November, December and January.

The second part of the paper contains detailed descriptions of the 600 fish in our collection. For each of the 52 species represented taxonomic notes are given,

and these include descriptions of five new species, the redescription of one species, the amalgamation of two species and modifications or enlargements to the descriptions of 24 others. Ecological data, including notes on distribution, size, stomach contents and development of gonads, are also given for each species.

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An ecological survey of some Inland Saline Waters of Algeria.

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(With 2 Text-figures)

INTRODUCTION.

Like terrestrial organisms in deserts, aquatic organisms in very saline waters are confronted by the problem of obtaining and maintaining an adequate water supply. As far as is known, living matter cannot function if its saline constituents are much more concentrated than sea-water, and life in high salinities thus entails extracting water against powerful osmotic forces. *Artemia salina* and the mosquito larva *Aedes detritus* can do this against an opposing pressure of 30–50 atmos. (Medewewa, 1927 ; Beadle, 1939). It is, therefore, not surprising that few organisms have been able to adapt themselves to extreme salinities, but those which have succeeded are often found in enormous numbers, partly no doubt owing to lack of competition.

Florentin (1899) and Thienemann (1913) reported on the maximum salinities in which various species were found in some Central European waters. But our knowledge of the ecology of this type of habitat is scanty, and, apart from the measurements of blood concentration in *Artemia* by Medewewa (1927), the physiology of high salinity adaptation is untouched. The present paper is a record of ecological work done on an expedition to Algeria during the first three months of 1938. Experimental work on salinity adaptation in the mosquito larva *Aedes detritus* has already been published (Beadle, 1939). It will be seen that the Northern Algerian Sahara is a particularly suitable field for such work, because a large number of patches of salt water with a wide range of salinity are concentrated in a comparatively small area (the Oued Rhir).

I was accompanied by my wife, whose assistance with both laboratory and field work was invaluable. We were fortunate in the excellent facilities available in the Laboratoire de Biologie in the University of Algiers, and I am very much indebted to Prof. M. Rose and Mlle H. Hamon and to their laboratory assistant, M. Raffoux, for their great hospitality and for the endless trouble they took on our behalf. I also received some useful advice from Dr. and Mme Gauthier, whose works on the fauna and flora of North African inland waters were indispensable (Gauthier, 1928 ; Gauthier-Lièvre, 1931). To Mr. Tracy Phillips I am especially grateful for an introduction to the administrative authorities in Algiers, without whose recommendations we should never have reached our objectives in the time available.

The expedition was supported by grants from the Government Grants Committee of the Royal Society, from the British Association and from the British Museum of Natural History. For a term's leave of absence I am indebted to the Council of the University of Durham College of Medicine.

In spite of other favourable circumstances, time was not sufficient for ecological work as thorough as originally intended. About five weeks were available for field work, and much of this was spent in moving from place to place. The remainder of the time was occupied in the laboratory and on the main journeys. I therefore decided to visit as many localities as possible for collection of the fauna and flora, and to confine the projected scheme for chemical work to those determinations which were *a priori* most likely to be of interest. In this way I hoped to discover some of the main problems to be solved, which, on a subsequent occasion, might be attacked more thoroughly.

METHODS.

Water Samples. Most of the waters were very shallow and samples were taken at the surface in glass bottles. In a few cases deeper samples were got by lowering a reagent bottle enclosed in a metal container rapidly to the required depth. This container was fitted with water inlet and air outlet tubes in such a way that the bottle was thoroughly washed through and finally contained the last water to enter.

Salinity was estimated in the field as density by glass hydrometers and corrected for temperature to the standard 1,000 for distilled water at 16° C. The variations in density encountered were enormous and the hydrometers were shown to be accurate to the nearest 0001. Sea-water has a density of approximately 1022.

Hydrogen ion concentration by phosphate buffers in sealed glass tubes.

Alkalinity by titration with suitable standard HCl solutions to the methyl orange end-point. None of the waters was alkaline to the phenolphthalein end-point.

Dissolved oxygen by Alsterberg's modification of the Winkler method, by which reducing substances are removed by preliminary bromination (Alsterberg, 1926). The presence of sulphide in several samples made this precaution essential. Owing to the abundance of phytoplankton it was obvious that dissolved oxygen was never an important limiting factor. The number of determinations was therefore reduced to a minimum.

Chloride by titration with suitable standards of silver nitrate, the sample having previously been diluted if necessary.

Complete analyses.

Estimations of the common inorganic ions were made at home on fifteen representative samples (Table II). For reasons of transport, samples could be no larger than 500 ml., and thus much smaller than required for the usual methods of water analysis. For the present purpose, however, this was of no disadvantage, because, owing to the high salinity, only small quantities were required. For Na and K semi-micromethods were used. The absolute error (in gm./l.) was, of course, much higher than with the standard methods of analysis on ordinary fresh waters. But the errors, which varied with the extent to which the sample had to be diluted and thus with the original salinity, were never high enough to alter significantly the figures for the relative composition expressed as percentage of the total weight of ions (Table II). Except for Ca, in sample 19 (see below), all ions were present in high concentrations. It was, therefore, the relative ionic concentrations which were likely to be of interest.

Ca, Mg and SO_4. By Hamer's modification of Blächer's method (Hamer, 1935). I am indebted to Dr. C. Mallen for suggesting this method and for advice upon its use. Three CO_3-free and carefully neutralised samples are titrated against standard potassium palmitate, (i) without further treatment, giving the concentration of Ca+Mg ; (ii) after precipitation of Ca with excess sodium oxalate, giving the concentration of Mg ; (iii) after the addition of a known quantity of standard $BaCl_2$, giving the concentration of Ca+Mg+Ba (not precipitated as $BaSO_4$). This method is very rapid and, with a little practice in the end-point, was found satisfactory for the present purpose, that is for estimating high concentrations of these ions. But in sample 19 (Table II) the concentration of Ca was so low that in a volume small enough for the estimation of Mg and SO_4 the error was greater than the actual concentration of Ca. Though the relative concentration of Ca was in any case insignificant, the extent to which the absolute concentration can be reduced in very saline water was of some possible biological interest. It was therefore estimated by the usual method whereby the oxalate is titrated with standard potassium permanganate (Thresh and Beale, 1933).

Na. By weighing as sodium zinc-uranyl-acetate in a sintered glass crucible. The procedure was based on that described by Mitchell and Ward (1932), but the

Station.	Date.	Time.	Temp. (° C.).	Density.	pH.	Alkalinity (N).	Cl. gm./l.	Remarks.
North Coast, near Oran.								
1. Dayet Morselli. Shallow lake, 6 kms. S.E. of Oran..	24.1.38	12.00	11	1029	7·7	0·0010	—	O_2 8·7 cc./l. Water yellowish. Total analysis, Table II.
2*a*. Shallow pools near S.E. shore of 1	24.1.38	11.30	10	1019	7·7	0·0094	12·65	O_2 17·0 cc./l. Water cloudy. Total analysis, Table II.
2*b*. ,, ,, ,, ,, ,, ...	,,	11.30	13	1024	8·4	0·0054	—	Water cloudy.
2*c*. ,, ,, ,, ,, ,, ...	27.1.38	09.30	9	1016	7·7	0·0058	—	—
2*d*. ,, ,, ,, ,, ,, ...	,,	09.30	10	1026	7·8	—	—	Water cloudy.
2*e*. ,, ,, ,, ,, ,, ...	,,	09.30	11	1063	8·4	0·0115	43·76	Water brownish and cloudy. Total analysis, Table II.
3. Sebkha d'Oran, petit bras de Valmy	25.1.38	09.00	8	1016	8·8	0·0012	8·37	Total analysis, Table II.
4. Pool S.E. of 3, on road to St. Maur.....	,,	10.15	12	1010	8·0	0·0029	—	Water cloudy.
5. ,, ,, ,, ,, ...	,,	11.00	12	1012	8·3	0·0046	—	—
6*a*. Dayet Oum er Relaz, lake 5 kms. from Ste Barbe du Telat on road to Arzew. Reed zone at E. end	26.1.38	08.45	18	1007	7·9	0·0023	3·23	—
7. Salines d'Arzew, large expanse of saline mud with patches of very shallow water.....	,,	11.15	19	1109	8·3	0·0024	86·10	Total analysis, Table II.
Between Constantine and Biskra.								
8. Les Lacs, lake W. of road c. 50 kms. from Constantine	10.2.38	12.00	11	1068	—	0·0030	35·50	—
9. Fontaine Chaude, 30 kms. N.E. of Batna	,,	15.00	23	1001	—	0·0070	0·27	Strong smell of H_2S in mud.
Biskra and southwards.								
11*a*. Hammam es Salahine, 5 kms. N.W. of Biskra, spring supplying 'Station Thermale'	11.2.38	16.30	42	1008	7·5	—	—	—
11*b*. 1 km. down stream derived from 11*a*.....	,,	16.30	14	1008	8·2	—	—	—
11*c*. Small channel derived from and close to 11*a*.....	,,	12.30	35	—	—	—	—	—
12. Touggouert. Stagnant irrigation channel (séguia)...	13.2.38	16.00	15	1028	8·5	0·0118	0·42	—
13. ,, Fast flowing channel (khandeg)	,,	16.00	12	1007	8·0	—	—	—
14. ,, Small lake at S. edge of oasis close to Temacine road	,,	16.00	12	1019	8·3	0·0060	9·65	—
14*a*. ,, Channel flowing from 14.....	,,	16.00	12	1013	8·3	—	—	—
15. ,, Khandeg	,,	16.00	12	1009	8·3	—	—	—
16*a*. Stagnant channel W. of Temacine road c. 5 kms. S. of Touggouert.....	14.2.38	10.00	9	1022	8·7	—	—	—
16*b*. ,, ,, E. of road	,,	16.00	12·5	1017	8·5	0·0061	8·00	See p. 230.
17. Lac Temacine, 15 kms. S. of Touggouert	,,	13.30	9	1011	8·3	0·0050	5·32	—
18. Lac Merdjadja, amongst sand dunes 5 kms. S. of Touggouert.....	15.2.38	11.30	10	1030	8·3	0·0031	16·93	[See p. 228. Total analysis, Table II.
19. Shallow pan receiving overflow from 18.....	,,	11.30	13	1040	8·3	0·0035	23·40	Total analysis of bottom water, Table II. See p. 228.
21. Meggarine N. lake, 15 kms. N. of Touggouert	16.2.38	10.30	13	1020	8·8	0·0069	9·77	—
21*a*. Stagnant channel near W. shore of 21	,,	11.00	14	1007	—	—	—	—
22. Meggarine S. lake	,,	12.00	15·5	1048	8·8	0·0132	29·20	See p. 229.
23. Stagnant channel N. of 21	,,	13.00	13	1017	—	—	—	—
27. Ain Zergs, Teghididine. Small lake 30 kms. N. of Touggouert.....	19.2.38	12.30	14	1005	8·5	0·0022	1·53	See p. 228.
28. Shallow pool formed by seepage from 27	,,	12.30	15	1008	7·8	—	—	Water smelling of H_2S. See p. 230.
29. Boughrioule, pond E. of road 2 kms. N. of Djamaa ..	,,	13.30	14	1007	8·5	—	—	—
30. ,, pond 100 m. N.E. of 29	,,	15.15	16·5	1006	8·5	—	—	—
31. Large expanse of shallow water, 0·5 km. S. of Djamaa	19.2.38	16.00	20	1025	9·0	0·0042	13·28	—
32. Touggouert. Irrigation channel W. of oasis	20.2.38	—	—	1005	—	—	—	[See p. 230.
33. 'Square Bresson'. Pool at base of crater-like depression in sand, 85 kms. S. of Touggouert	21.2.38	14.00	16	1031	8·7	0·0190	15·45	Total analysis, Table II. Water brownish, smelling of H_2S.
33*a*. Well in depression, 10 m. from edge of 33; water surface 4 m. down	,,	15.30	15	1007	8·0	0·0069	2·48	Total analysis, Table II. See p. 230.
35. Ouargla Chott. Large expanse of shallow water, 4 kms. W. of Ouargla oasis	23.2.38	10.00	13	1054	8·5	0·0044	32·00	[See p. 226. Total analysis, Table II.
36. Channel flowing into 35	,,	10.00	14	1008	8·3	—	—	—
37. Ain Beida. Small spring in sand dune, 8 kms. S. of Ouargla	,,	11.30	22	1001	8·0	—	—	—
38. Stagnant channel on N. side of Touggouert road, 8 kms. from Ouargla	,,	15.00	19·5	1008	9·0	—	—	—
39. El Golea. Fast flowing channel derived from 41....	26.2.38	10.00	26	1000	—	—	—	—
40. ,, Small lake N. of oasis derived by seepage from 41	,,	10.30	11	1005	9·2	—	—	—
41*a*. ,, Artificial lake fed by artesian boring (26° C.), north shore	,,	10.30	12.5	1000	8·2	—	—	—
41*b*. ,, Artificial lake close to boring	,,	11.30	19	1000	—	—	—	Water slightly smelling of H_2S.
43. ,, Small shallow pond derived from 44.....	,,	17.00	16	1009	8·5	—	—	—
44. ,, Bel Bachir, artesian boring 1 km. N. of 40.	27.2.38	09.00	26	1000	8·3	—	—	—
45. ,, Hassi el Abid. Well 15 kms. N. of oasis.. Water surface 7 m. down	,,	11.15	22	1000	8·0	—	—	—
46. ,, Sebkha el Melah. Long shallow expanse due to overflow from oasis.....	,,	16.30	17	1002	8·5	—	—	Water slightly cloudy.
50. Hassi Iniguel. Well on Ouargla road, 35 kms. from El Golea. Water surface 20 m. down	28.2.38	16.00	22	1000	8·0	—	—	Water at 20 m.
52. Hassi Sahane. Well on Touggouert road, 55 kms. from Ouargla. Water surface 9 m. down	2.3.38	16.00	23	1002	8·0	0·0025	1·42	Water at 9 m. Marked 'Eau magnésienne potable.' Total analysis, Table II. [salée'.
53. Hassi Ali ben Salah. Well, 105 kms. from Touggouert. Water surface 2 m. down	3.3.38	09.00	12.5	1010	8·3	—	—	Water at 2 m. Marked 'Eau
54. Hassi Butana. Well, 30 kms. from Touggouert. Water surface 3 m. down	,,	10.30	12	1006	8·2	0·0034	1·17	Water at 3 m., cloudy and foul. Marked 'Eau magnésienne potable.' Total analysis, Table II. [p. 227.
55. Ourlana. 35 kms. N. of Touggouert. Bahr Inférieur. (small lake).....	4.3.38	11.30	14·5	1010	8·3	0·0056	4·30	Total analysis, Table II. See
55*a*. ,, Small pool, due to seepage from 55	,,	11.30	—	1057	8·7	0·0081	36·00	Total analysis, Table II. Water cloudy. [See p. 227.
55*b*. ,, Fast flowing channel connecting 55 and 56	,,	15.00	—	1004	—	—	—	—
56. ,, Bahr Supérieur.....	,,	15.00	19	1004	8·3	—	—	—
57. Touggouert. Main artesian boring in centre of oasis.	6.3.38	08.30	25	1003	7·5	0·0023	—	Saturated with CO_2, O_2 3·27 cc./l. Total analysis, Table II. See p. 238.
58. ,, Irrigation channel E. of oasis	,,	—	—	1005	—	—	—	—
59. ,, Irrigation channel in garden flowing from 57	,,	—	—	1003	—	—	—	—
60. El Arfiane. 80 kms. N. of Touggouert. Irrigation channel	7.3.38	11.00	24·5	1003	8·3	—	—	—
61. El Bachir. Group of shallow lakes, 3 kms. S. of Tolga, 35 kms. S.W. of Biskra	9.3.38	08.00	12	1058	9·1	0·0127	12·50	Total analysis, Table II.
62. ,, ,, ,, ,, ,, ,,	,,	09.00	14	1058	—	—	—	—
65. ,, ,, ,, ,, ,, ,,	,,	10.00	23	1052	—	—	—	—
66. Ain Zerga. Small very deep pond, 3 kms. S. of El Bordj, 5 kms. W. of Tolga	,,	15.00	19	1001	8·1	—	—	—

TABLE II.

Station.	Density.	Alkalinity.	*p*H.	$Na^{\cdot}$.	$K^{\cdot}$.	$Ca^{\cdot}$.	$Mg^{\cdot}$.	Cl^{-}.	SO_4^{-}.	Sum.
				expressed as grams per litre.						
1*a*	1029	0·0010	7·8	8·20 *22·9*	0·412 *1·1*	1·16 *3·2*	1·80 *5·0*	17·84 *49·8*	6·40 *17·9*	35·81
2*a*	1019	0·0094	7·7	5·31 *19·9*	0·274 *1·0*	1·03 *3·8*	1·66 *6·2*	12·65 *47·3*	5·76 *21·6*	26·68
2*e*	1063	0·0115	8·4	18·50 *21·3*	0·620 *0·7*	1·08 *1·2*	5·56 *6·4*	43·75 *50·5*	17·40 *20·0*	86·91
3	1016	0·0012	8·8	4·68 *23·8*	0·015 *0·1*	0·72 *3·7*	0·79 *4·0*	8·37 *42·5*	5·09 *25·8*	19·66
7	1109	0·0024	8·3	33·00 *24·2*	0·569 *0·4*	3·54 *2·6*	7·78 *5·7*	86·10 *63·0*	5·28 *3·97*	136·27
18	1030	0·0031	8·3	8·63 *20·8*	0·816 *2·0*	1·52 *3·7*	1·94 *4·7*	16·93 *40·9*	11·62 *28·2*	41·46
19	1170	0·0180	9·0	62·30 *23·9*	3·56 *1·4*	0·038 *0·0*	10·3 *3·9*	63·5 *62·5*	21·75 *8·3*	261·41
35	1050	0·0044	8·5	19·18 *28·3*	0·980 *1·4*	1·08 *1·6*	1·94 *2·9*	34·60 *51·1*	10·04 *14·8*	67·82
33*a*	1007	0·0069	8·0	1·28 *15·6*	0·095 *1·2*	0·84 *10·2*	0·34 *4·1*	2·48 *30·2*	3·17 *38·6*	8·20
33	1031	0·0190	8·7	9·40 *25·2*	0·462 *1·2*	0·92 *2·5*	2·06 *5·5*	15·45 *41·5*	8·93 *24·0*	37·22
55	1010	0·0056	8·3	1·89 *15·8*	0·094 *0·8*	0·88 *7·4*	0·74 *6·2*	4·30 *36·0*	4·03 *33·7*	11·94
55*a*	1057	0·0081	8·7	19·20 *25·1*	0·530 *1·4*	1·16 *1·5*	4·53 *5·9*	36·00 *47·1*	15·00 *19·6*	76·42
52	1002	0·0025	8·0	0·57 *12·5*	0·075 *1·6*	0·40 *8·8*	0·35 *7·7*	1·42 *31·2*	1·74 *38·2*	4·55
54	1006	0·0034	8·2	0·58 *10·2*	0·142 *2·5*	0·60 *10·0*	0·34 *5·9*	1·17 *20·0*	2·88 *50·0*	5·74
57*	1002	0·0023	8·1	0·80 *18·1*	0·027 *0·6*	0·53 *12·0*	0·19 *4·4*	1·20 *27·2*	1·65 *37·5*	4·40
61	1058	0·0127	9·1	9·51 *13·7*	0·735 *1·1*	0·20 *0·3*	6·60 *9·5*	12·50 *18·0*	40·03 *57·9*	69·57
Sea-water	1022	0·0025	8·2	10·70 *30·5*	0·390 *1·1*	0·42 *1·2*	1·31 *3·7*	19·64 *56·0*	2·69 *7·6*	35·15 [CO_3 0·119]
Wembury Stream†	—	0·0040	7·8	0·025 *7·9*	0·019 *6·3*	0·065 *21·0*	0·014 *4·7*	0·041 *13·4*	0·025 *7·9*	0·308 *38·6*

Figures in italics represent relative concentration expressed as percentage of the total weight of ions.

* Figures for ionic concentrations kindly supplied by M. Bertrand, Govt. Hydrologist at Touggouert.

† From Pantin (1931).

precipitation was done in the same crucible, with a rubber bung in the lower end to prevent leakage through the sinter. 1 ml. of the sample was used, which, in most cases, was previously diluted.

K. By the method commonly employed for blood (Peters and van Slyke, 1932), in which 1 ml. samples are used, and the potassium is estimated as the centrifuged cobaltinitrite precipitate by titration with permanganate.

Collections and identification.

Collecting was done with hand plankton and coarse-meshed nets. Mud-living organisms were got in shallow water by sifting the mud or (for surface mud diatoms and algae) by putting it direct into specimen tubes. Mud from deeper water was collected by throwing out a small hand dredge from the shore. Owing to the unusual lateness of the hot season, we were unable to get full-grown specimens of cyprinoid fish from the Oued Rhir. During the cold weather they appear to hide at the bottom of the deeper pools. The Arabs, whom we employed at Touggouert for this purpose, could catch only small specimens. But *Cyprinodon fasciatus* was not affected, and could always be caught in shallow water with a hand net. It was not possible to estimate accurately the numbers of a given species. But a very rough idea of the relative abundance is given in Table IV.

I am very much indebted to the following specialists for reporting on the collections of the groups mentioned :—

Copepoda : Dr. F. Kiefer (systematic report completed, but unpublished).
Phyllopoda : Dr. J. P. Harding.
Mollusca : Dr. G. I. Crawford.
Hydrachnida : Dr. C. Walter (systematic report already published, Walter 1940).
Mosquito larvae : Dr. G. Senevet.
Ephydridae : Dr. G. C. Lamb (through Dr. W. H. Thorpe).
Amphibia : Dr. H. W. Parker.
Rhabdocoelida : Mr. J. B. Cragg.

Prof. P. de Beauchamp kindly advised me concerning one or two of the more doubtful Rotifera. The saline water Rotifera of French N. Africa had not previously been examined in any detail. For the identification of the Cladocera the works of Gurney (1909) and Gauthier (1928), together with references given by them, were the main sources of information. To Dr. K. B. Blackburn I am much obliged for advice and literature which enabled me to make a general survey of the algal flora (exclusive of diatoms). Practically nothing is known of the saline water diatoms of this region, and it is unfortunate that a report on this collection, which was the largest of all, could not be included here. The presence of the marine genus *Chaetoceras* is, however, noted. Dr. Ross's report on both this and Prof. Omer-Cooper's collection from Siwa in the Egyptian desert should be of great interest. Foraminifera were noted in some of the mud samples from the Oued Rhir. These have been sent to Dr. Heron Allen.

General account of the localities visited.

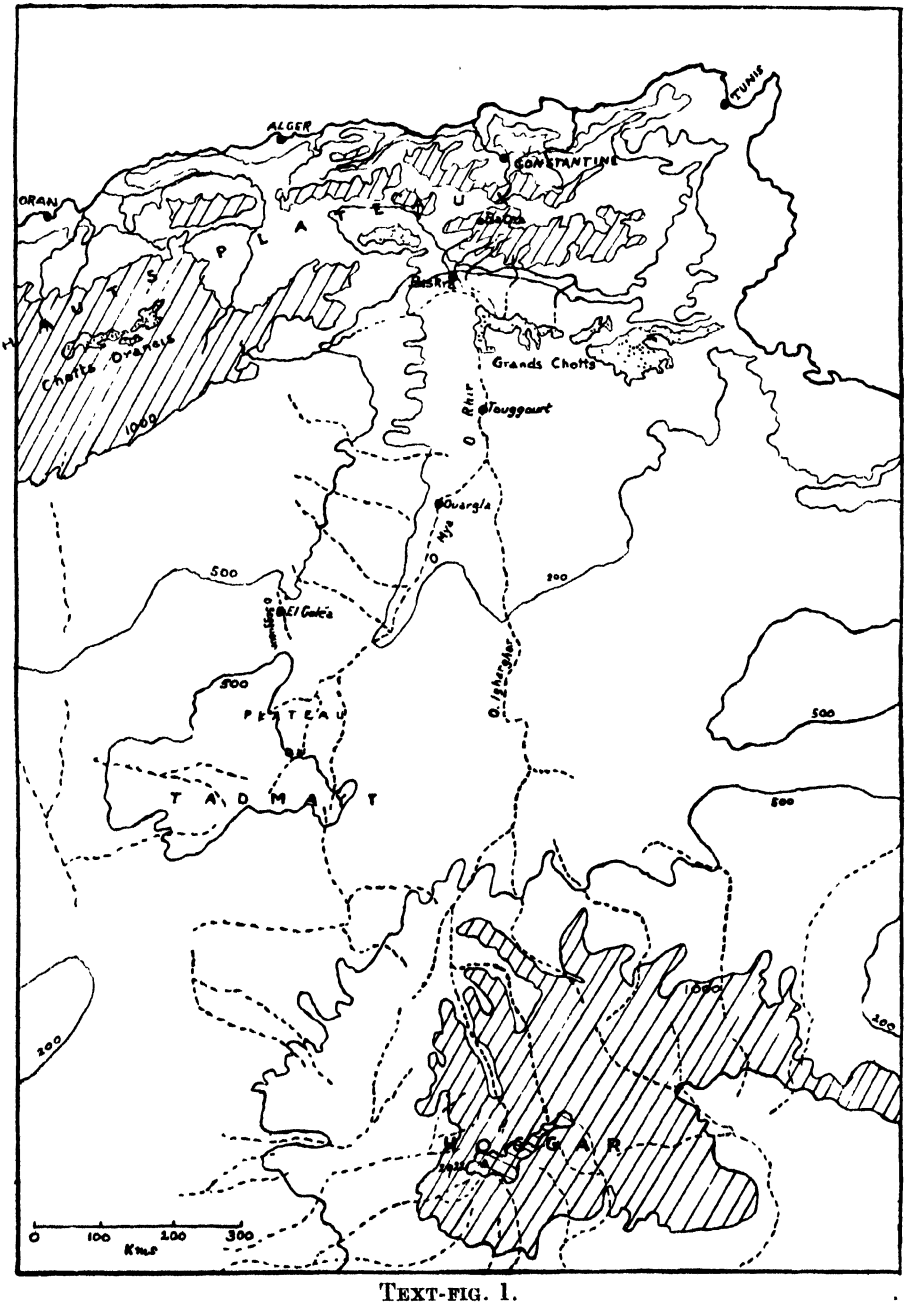
Travelling was done in a second-hand car bought in Algiers. The roads in the north are excellent, but south of the Atlas our progress was naturally hampered by the usual difficulties of desert travelling in a car not especially adapted for the purpose. Two districts were visited (see text-fig. 1) : (i) Oran, on the north coast within a few kilometres of which are several saline lakes and pools ; (ii) The Oued Rhir, in the northern Algerian Sahara, with a centre at Touggouert, which lies about 200 km. southwards into the desert from Biskra. A short visit was made *via* Ouargla to El Golea, about 450 km. south-west of Touggouert.

Oran.

On the coastal plain behind and east of Oran are several patches of standing water of varying degrees of salinity. Some, such as the Salines d'Arzew (7), which was the most saline water encountered in this district, are exploited commercially for salt. Unlike the exposed waters of the desert (see below) these owe their high salinity primarily to leaching of the salt-bearing triassic rocks (Gautier, 1922 *a*). Subsequent evaporation plays a relatively small part except in the height of the summer.

The Oued Rhir.

Most of the work was done in this region, which, though desert, contains many patches of open water, temporary and permanent, natural and artificial. The hydrography and past geological history of the Oued (=Wadi) Rhir, which is an ancient river-bed, are of great interest to the biologist and have been well summarized by Gautier (1922 *a*, *b*, 1928). Prior to the Pliocene and before the uprising of the Atlas Mountains, the Northern Sahara was invaded by the sea several times and to varying extents. The maximum southern extension of the sea, which included El Golea, occurred in the Eocene. The presence of living marine organisms in the waters of the Oued Rhir, such as Foraminifera (Gauthier-Lièvre, 1935), the diatom *Chaetoceras* (Gauthier-Lièvre, 1931) and *Palaemonetes varians* (Gauthier, 1928; Gurney, 1909), must be referred back at least to the Miocene if they are to be considered as marine relicts and not in some manner to have been transported later. During the Quaternary Epoch it is generally agreed that the Oued Rhir formed the lower reaches of a river, the Oued Igharghar, which flowed from the Hoggar Mountains northwards to the foot of the Atlas (text-fig. 1). Here it was joined by the Oued Djedi, which still flows after rains in the Atlas, and formed a large lake in a closed drainage basin with no outlet to the sea, the remains of which are still to be seen in the Chotts north-east of Touggouert. The Oued Igharghar was one of several quaternary rivers which radiated in all directions from the Hoggar Massif, and thus, like the Nile today, formed a bridge between Central and Northern Africa for the passage of animals not adapted to desert conditions. This would account for the presence in the highlands of French North Africa of certain Central African elements in the fauna, some of which, such as the Elephant, are now extinct, and for the remarkable discovery of *Crocodilus niloticus* living in a pool on the slopes of the Hoggar Mountains, now isolated on all sides by immense tracts of desert (Seurat, 1934). These rivers are now dead as far as surface flow is concerned, except at their heads, which discharge the rains precipitated on the Hoggar Mountains into the sands of the Sahara. But they still mark the course of a flow of underground water. In the Oued Igharghar this water seeps very slowly northwards, some 800 km.to the foot of the Atlas, and with the Oued Djedi still preserves the last remnants of the ancient lake (Les Grands Chotts). In its lower reaches (Oued Rhir) there are several natural upwellings to form small, permanent lakes (Bahr, plur. Behour), which form a curious contrast with the surrounding desert. Owing to the abundance of underground water, the Oued Rhir supports a large number of oases which centre round Touggouert and produce the bulk of the Algerian dates. Water-bearing strata occur at different depths and can be tapped at high pressure by artesian boring. The most superficial water is got by drawing from wells. It is conveyed by main channels (Khandegs) through the plantations (Palmeraies), and is diverted when required through smaller side channels (Séguias) at a lower level which flood the roots of the palms. The Khandegs are usually fast-flowing and not appreciably more saline than the source, whereas the Séguias often become stagnant and very saline by evaporation. In some oases there is a large excess of water which, in the cool winter season, collects as a shallow expanse (Sebkha) below the oasis, becomes saline by evaporation and often dry in summer. Such places form temporary feeding grounds for aquatic birds, such as ducks, spoonbills, flamingoes and waders.


ALGER
TUNIS
CONSTANTINE
ORAN
HAUTS PLATEAUX
Chotts Ouargla
Grands Chotts
Biskra
Touggourt
Ouargla
El Goléa
1000
500
300
200
TADMAIT
ERG
0 100 200 300
Kms

TEXT-FIG. 1.

The salinity of the artesian water at the source varies considerably in different places, but the high salinity of the standing water derived from it is primarily due to evaporation. The small natural lakes (Behour), mentioned above, were presumably formed by faults reaching the water-table. Such are Merdjadja (18), Temacine (17), Meggarine (21 and 22), Square Bresson (33), Ourlana (55 and 56), and Ain Zerga (66). These are in some cases of considerable depth, and such permanent lakes must have been in existence since Quaternary times, as is suggested by the presence of Central African fish, such as *Clarias lazera*, *Tilapia zilli*, *T. galilaea*, *Hemichromis bimaculatus*, and *Astotilapia desfontainesi* (Pellegrin, 1921).

The oasis of *Ouargla* is situated in the Oued Mya, an ancient tributary of the Oued Rhir (text-fig. 1). The irrigation water is here fresh at the source, but finally collects in a large shallow expanse, Ouargla Chott (35), which is extremely saline even in winter.

El Golea was the southernmost point reached by us. It is situated on higher ground east of the Oued Mya and, properly speaking, outside the Oued Rhir water system. The freshness and luxuriance of the vegetation in this attractive oasis are due to the abundance of pure fresh water. This issues from borings into the bed of the Oued Seggueur. One of these collects at first in a small lake (41), whence it circulates through the irrigation channels. The excess collects south of the oasis as a large shallow expanse, Sebkha el Melah (46), where evaporation, even in winter, is sufficient to render it appreciably saline.

Thermal waters.

There are a number of thermal springs in various parts of Algeria. Two of these, which are also saline, were visited en route to the desert. Fontaine Chaude (9) is a spring of constant temperature about 23° C. on the road from Constantine to Batna. It is very slightly saline and is noted for being one of the two localities in which is found the curious cyprinodont fish, *Tellia apoda*, devoid of pelvic fins. This is a near relative of *Cyprinodon fasciatus*, which is common in the saline waters of the Oued Rhir.

Hammam Salahine (11) is a larger and hotter spring (41° C.) close to Biskra. It is also more saline and is used for medicinal baths. The spring wells up from the bottom of a large pool and flows down a stream in which collections were made.

Desert wells.

Plankton collections were made in a few isolated wells (45, 50, 52, 53, 54) on the journey Touggouert-Ouargla-El Golea. This was done by lowering a bucket and filtering the water through a plankton net. Such wells are interesting, both for the variation in composition of their water and for their extreme isolation. In the absence of strong light and with a relatively constant temperature, the fauna and flora are probably influenced mainly by the chemical composition of the water. But there is always the unknown factor of contamination by travellers.

General chemical characteristics of the waters.

The salinities, as estimated by density, range from 1000 (39, 45, 50) to 1172 (19), i.e. from fresh water to about eight times the salinity of sea-water. Station 19 is, however, well outside the range of the majority which extends between 1002 and 1030, though eight samples range from 1048 to 1070.

The range of *p*H found was 7·5–9·2, which is not abnormal for natural waters. The alkalinity range (0·001–0·018 N) indicates that they are buffered to about the same extent as sea or a hard fresh water (Table I; see also p. 238). The absolute concentrations of CO_3, as roughly indicated by the alkalinity figures, are of the same order as in sea or a hard fresh water, but it follows that the relative concentrations, expressed as percentage of the total weight of ions, are very low in all but the fresh water. This is correlated with a low relative concentration of Ca,

and is no doubt due to the precipitation of $CaCO_3$ with increasing salinity. The distinguishing feature of the Algerian waters is the high concentration of SO_4 which, when compared with sea-water, partly replaces Cl (Table II). In an extreme case (61) there is as much as 40 gm./l. SO_4, which amounts to 58 per cent. of the total weight of ions. As would be expected, increasing salinity is correlated with a lowering of the relative concentration of SO_4 together with that of Ca, due to precipitation of $CaSO_4$. In the most saline sample (19) the concentration of Ca was lowest. The abundance of gypsum deposits in North Africa is well known.

The effects of evaporation on chemical composition were more certainly demonstrated by comparing two waters derived from the same source but having suffered different degrees of evaporation. This was done on two occasions: (i) Station 33 (Square Bresson) was a small pond at the bottom of a natural depression in the sand reaching the water-table. This water was well exposed for evaporation, whereas a well (33 *a*) dug within a few yards of the pond into the same water-table was more protected and contained water less than a quarter the salinity of the pond. (ii) The Bahr Inférieur at Ourlana (55) is the lower of two small natural lakes continuously fed by a stream of water up-welling from the bed of the Bahr Supérieur (56). Within about 2 m. of the edge of 55, at the time of our visit, was a small pool (55 *a*), obviously formed by the seepage of water from the lake into a small, probably artificial, depression. The water in 55*a*, being out of the main stream, had become concentrated about six times. Comparing 33*a* with 33 and 55 with 55*a* (Table II) it is clear that evaporation has caused a decreased relative concentration of Ca and SO_4, and this, as expected, is accompanied by an increased relative concentration of Na and Cl.

Many of the desert waters, particularly in the Oued Rhir, are classed as 'eaux magnésiennes'. This applies to the two wells (52) and (54) as well as to the main artesian water at Touggouert (57), which are termed 'eaux magnésiennes potables'. The intestinal disorders contracted by those who are not accustomed to it are said to be due to the high magnesium content. The analyses of these three waters (Table II) do not indicate an abnormally high relative concentration of Mg, but since the salinity is 15 to 20 times that of a normal fresh water, the absolute concentration of Mg is correspondingly high. Sea-water diluted to the same salinity would have a similar composition except for a lower SO_4 and higher Cl content.

Though the samples analysed in Table II are from waters widely separated over the areas visited, they all show the same general characteristics. The differences are mainly attributable to the effects of concentration. These waters are, in fact, of the sulphato-chloride type (Clarke, 1924). Except where extreme concentration has altered the proportions, the relative concentrations of SO_4 and Cl are high, the former preponderating; that of CO_3 is low.

There is no *a priori* reason for supposing that, apart from total salinity, there is anything in the composition of these waters likely to act directly as a biologically limiting factor. A possible exception is the low Ca concentration in the most saline sample (19). The absolute concentration (0·038 gm./l.) is, however, higher than in some very soft fresh waters (e.g. Loch Lomond, c. 0·004 gm./l.) which support a normal fauna and flora. But it is quite possible that a certain ionic balance is more important for life in saline than in fresh waters, and that, in fact, a low relative concentration of Ca in reducing resistance to the effects of high salinity, may constitute a limiting factor for some organisms, though the rotifer *Brachionus plicatilis* (*müller*) can apparently live in Ca-free sea-water (Worley, 1929). This can only be settled by experiment. Ostwald (see Höber, 1926, p. 666), using concentrations higher than fresh water, found that the freshwater *Gammarus pulex* could withstand stronger salt solutions if these were 'balanced', whereas Beadle and Cragg (1940 and unpublished) have shown that it can live for long periods in pure NaCl solutions, when of the same order of concentration as fresh water, and even in distilled water. Further experiments on these lines are obviously required.

Indirectly, the high concentration of SO_4 in these waters is likely to result in conditions of some biological importance. It is well known that under stagnant conditions H_2S can be formed from dissolved sulphate by bacterial action (Stephenson, 1930). The presence of H_2S even in quite shallow pools is evidence of this, and will be discussed below.

The biological effects of high salinity as such are likely to be two-fold. In the first place the fauna and flora will be limited to those forms possessing an efficient osmo-regulatory mechanism, and, secondly, an abundance of salts, coupled with the optimum light conditions of this region, is likely to favour the growth of phytoplankton. The great abundance of phytoplankton, especially diatoms, was certainly confirmed. As a result the waters, even when stagnant, were always well oxygenated (see section on Water Layering).

Water layering and H_2S production.

Without a boat we were unable to investigate thoroughly conditions at different depths. In the case of Ain Zerga, Tighididine (27), we made use of an overhanging bough to get water from the bottom at 2 m., and in Lac Merdjadja (18) a sample was got from 5 m. by swimming out from the shore. It was assumed that the temperature of samples from 5 m. or less did not alter by as much as 0·5° C. when drawn rapidly to the surface. A good indication of the temperature conditions at the bottom was also got by putting a thermometer into mud rapidly dragged up in the dredge thrown out from the shore.

It is well known that in the cold season it is difficult to catch full-grown specimens of the cichlid fish of the Oued Rhir, because they hide at the bottom of the deeper lakes, where the average temperature is generally higher and more uniform than at the surface. The cold weather was unusually late in 1938 and continued until after we had left the desert. The average maximum and minimum shade temperatures at Touggouert from 12–20 February 1938 were 17·2° and 3·3° C., from 3–7 March 20·5° and 4·0°. The more usual conditions are shown by the average monthly maxima and minima for the period 1916–20 :—February 19·7° and 6·3°, March 22·9° and 8·5°. For the hottest month (July) the average figures were 42·4° and 25·4° (Lasserre, 1922). We were therefore unable to observe the effects of the change of season, as we had hoped. But our few observations indicate some interesting problems which would repay further investigation.

The relevant data are recorded in Table III. In assessing the significance of the temperature figures attention should be given to the time of day. These waters were of two types :—(*a*) In the lakes Merdjadja (18) and Ain Zerga, Tighididine (27), density and chemical conditions did not change with depth, and the reversed temperature gradient in the morning was righted during the day, when the surface layers became warmer than the lower. Both these had subterranean inlets, as shown by the presence of an overflow and absence of a surface inlet. This would insure thorough mixing. (*b*) In the second type there was a stagnant layer of water at the bottom which was much more saline than that at the surface. A reversed temperature gradient, which was sometimes very steep, was maintained throughout the day. The latter would, of course, have been impossible but for the much greater density of the lower water.

The most remarkable example of the second type was Station 19, a very shallow expanse of water fed by the overflow from Merdjadja (18). Though only 0·3 m. deep, the bottom water was more than five times as dense and (at 2 p.m.) 12° hotter than the surface. The inflow was no more than a trickle, and there was no visible outflow. But the surface water, obviously directly derived from the inflow, may have been escaping at the edges by percolation through the sand. The underlying very saline water must have been stationary and unable to escape through salt-saturated mud. This condition may have been produced in the following manner. Both 18 and 19 are quite unshaded and in the open desert. During the hot season the rate of

evaporation must be enormous, and the inflow into 19, in winter only a trickle, would probably stop, with the result that 19 would be reduced to a dry mud-flat saturated with salt. The first flooding by the inflow in the subsequent cold season would dissolve the salt and form a layer of extremely saline water, over which the following water would flow without mixing. A comparison between the percentage compositions of 18 and of the lower layer of 19 (Table II) suggests that much $CaSO_4$ is deposited in the mud during this process. This would help to make the mud impermeable and so preserve the lower saline layer so long as it is covered by the upper less saline water. During the day it is probable that, even in the cold season, sufficient radiant heat could penetrate this shallow water to raise the temperature of the mud to more than 30° C. The stagnant layer overlying it would prevent the loss of heat at the surface, due to wind and evaporation, from affecting the mud. For the same reason heat loss at the surface during the night would have little effect on the lower layer. But observations during the change of seasons are required before this explanation can be shown to be the correct one.

TABLE III.

Station.	Date. Febr. 1938.	Time.	Depth.	Density.	Temp. (°C.).	*p*H.	Alkalinity (N).	O_2 (cc./l.).	Cl (gm./l.).
14	13	15.30	Surface	1019	16·0	8·3	0·0060	—	9·65
			1 m.	—	25·0 (mud)	—	—	—	—
16*b*	14	16.00	Surface	1017	12·5	8·5	0·0061	9·00 (7·90)*	8·00
			1 m.	1069	13·5	—	0·0052	3·30 (0·00)*	19·55
18	15	10.30	Surface	1030	14·0	8·6	0·0031	11·60	16·93
			5 m.	1030	15.0	8·6	0·0031	12·00	16·93
19	15	14.00	Surface	1033	19·0	8·5	0·0040	—	—
			0·3 m.	1172	31·0	9·0	0·0180	—	163·50
22	16	12.00	Surface	1048	15·5	8·8	0·0132	—	—
			2 m.	(crystal-lizing)	25·0	—	—	—	—
27	19	12.30	Surface	1005	14·0	8·5	0·0022	8·25	1·53
			2 m.	1005	13·0	8·5	0·0022	7·50	1·53

* Without preliminary bromination.

The very saline lower layer of 19 seemed to be toxic to most of the organisms living in 18. A few Diatoms, apparently alive, were found on the surface of the mud. The upper layer, however, contained numbers of the green Chlamydomonad flagellate common in 18, and several dead *Cyprinodon fasciatus* were floating on the surface. These were presumably washed in with the inflow from 18 and were killed by sudden contact with the highly saline lower water or died owing to lack of suitable food.

Station 19 was an extreme example of conditions which are apparently common in deeper waters of the Oued Rhir during the winter. In Meggarine S. Lake (22, Table III) the bottom at 2 m. was nearly 10° hotter than the surface, and was composed entirely of salt crystals, showing that the lower water was saturated. This lake, like 19, was fed by surface water and possessed no outlet. The temperature of the lower water was much less than that of 19, and this was no doubt due to the greater depth and volume, which would hinder the penetration of radiant heat from above. It is possible that the lower layer would conserve to a certain degree the heat gained during the previous hot season, at which time (according to the explanation given above) it would not be covered by a less saline layer and would be much reduced by evaporation. No organisms were found in the lower saline water nor

amongst the salt crystals at the bottom, but both Diatoms and Chlamydomonadales were abundant in the upper layer and on the mud at the edge.

A similar stratification was found in a stagnant irrigation channel (16*b*, Table III) near Touggouert. The water was a little over 1 m. deep and the lower half was about four times as dense as the upper. A sharp discontinuity layer could be seen at about 0·5 m. by stirring with a stick. There was a slight reversed temperature gradient at 2 p.m. This channel received water already used for irrigation, which would reach it at irregular intervals, since the plantations are flooded intermittently. It is probable that the lower water was received from an irrigation previous to the last one, and that it evaporated and became concentrated before the next inflow, which then floated on top and formed the upper layer. The water of the lower layer smelt strongly of H_2S, and it might have been expected that, like the bottom of the hypolimnion of a eutrophic lake, it would have been devoid of oxygen and unable to support aerobic life. It was found, on the contrary, to contain plenty of oxygen (3·30 cc./l.), though, owing to the H_2S, none could be detected without preliminary bromination (Table III). The plankton of the surface layer was very concentrated and included Diatoms, Myxophyceae, Rotifers, Copepods and Nematodes (Table IV). In the lower layer the plankton was not as rich, but was by normal standards fairly abundant, all the forms found at the surface, except Copepods, being represented. The H_2S was presumably being produced in the mud, mainly, perhaps, through reduction of sulphate by bacterial action. In any case, the mud must have been in a condition of extreme reduction. The accumulation of oxygen in the lower layer could only have been caused by a constant production in the water itself. The abundance of phytoplankton, especially Diatoms, in the lower layer would account for this, and in such shallow water, which was also quite clear, illumination would be intense.

Two examples were found in which there was no apparent density stratification, but where the water smelt strongly of H_2S, even at the surface. The overflow from Ain Zerga, Tighididine (27), formed a small marshy pool (28) about 0·3 m. deep, and the H_2S was, presumably, being formed in the soft black mud at the bottom. The oxygen content was not measured, but was no doubt plentiful, since the illumination was good and abundant Diatoms and Myxophyceae were present. Some Copepod nauplii, dragonfly larvae and the mollusc *Hydrobia brondeli* were also found. The second example was the pool (33), at the bottom of a crater-like depression in the sand between Touggouert and Ouargla, known as 'Square Bresson'. This was apparently a fault which had exposed the water-table. Thus there was no outlet or inlet in the ordinary sense, the level of the pool being maintained by the underlying water-table. The same water had been exposed by the digging of a well (33*a*) within a few metres of the pool, but exposure of the pond surface had caused a considerable rise of salinity as compared with the well-water, which was probably close in composition to the subterranean water. At the bottom of the pool was a deep and soft black mud—the probable seat of H_2S production, the smell of which was evident even in the surface water. As in 28, there was an abundance of phytoplankton, including Diatoms, *Euglena* and Myxophyceae, and the zooplankton included vast numbers of Rotifers and many Ephydrid and Tipulid larvae.

The production of H_2S in these waters seems to be associated more with the presence of a certain kind of soft and deep mud than with any other obvious factor. The simultaneous production of oxygen by photosynthesis is an unusual phenomenon, but several species of Diatoms have been recorded from water containing H_2S (Kolbe, 1932), and many Myxophyceae are well known to inhabit sulphur springs. It is therefore probable that stagnant water in deserts, unlike a tropical swamp (Carter and Beadle, 1931), is never likely to be low in dissolved oxygen, for the reason that it would normally be saline and intensely illuminated. These conditions favour an abundant growth of Diatoms, and the oxygenation due to photosynthesis would override the reducing effect of the mud.

There are obviously several interesting problems in this connexion which would repay further investigation. In the first place the origin of this curious stratified condition could be decided by observations at different seasons. Secondly the unstable equilibrium between (i) reduction and H_2S production in the mud and (ii) oxygenation by photosynthesis in the water in contact with it should be more thoroughly investigated. This might be done by simultaneous measurements of oxidation-reduction potential in the mud, and H_2S and O_2 concentrations in the water, during the day and also at night, when the production of O_2 would cease. And lastly, the effects of H_2S in the concentrations found, upon the respiratory metabolism of organisms able to live in such an environment might be a good subject for experiment. A comparison with its effects on other organisms might show some adaptation in the mechanism of respiration.

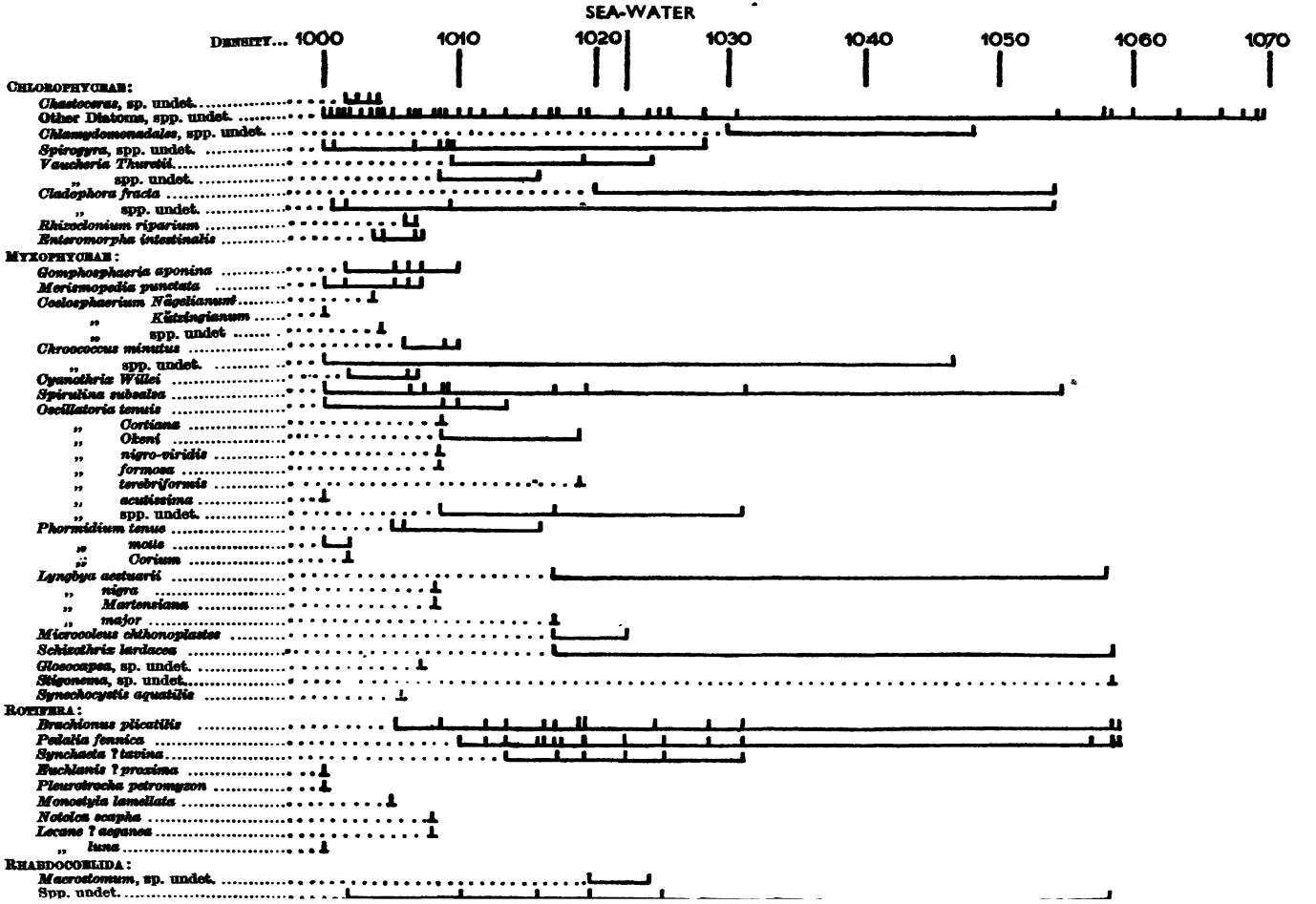
Distribution of fauna and flora.

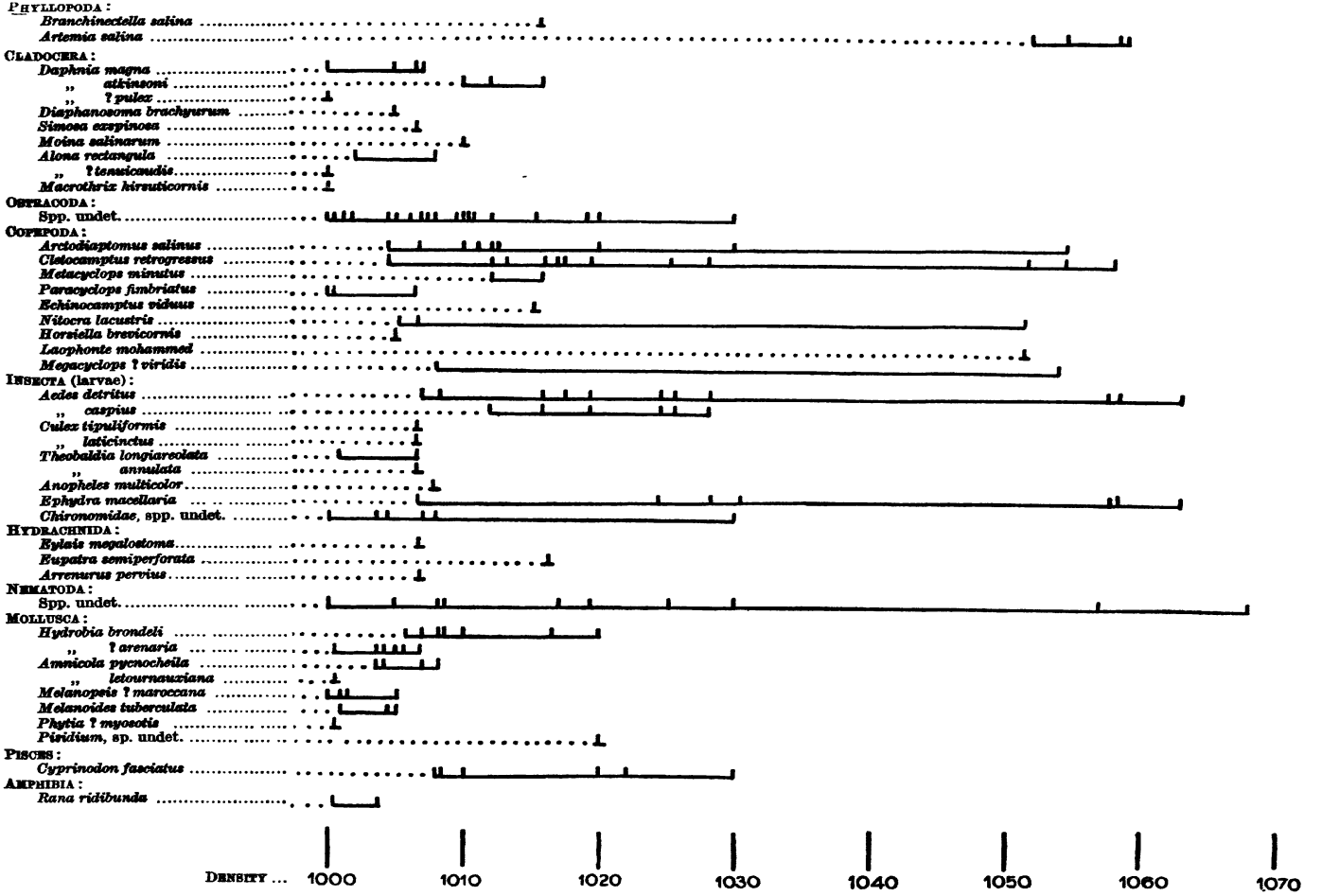
It is never safe to draw far-reaching conclusions from a single set of collections as to the effect of the environment upon the distribution of organisms. This is especially true of inland waters in which certain organisms may at one time be abundant and at another completely absent for reasons which we do not as yet understand. It is possible that environmental factors are not always responsible for such fluctuations, and that the life-history of some organisms may be partially directed by an internal physiological rhythm. On the other hand, if collections are made from a sufficient number of localities which differ primarily in respect of one factor (e.g. salinity), a general idea of the effect of variations in this factor can be obtained.

Table IV summarizes the records of all organisms found except Bacteria and Protozoa, and indicates where each was particularly abundant or scarce. In text-fig. 2 the records (short vertical lines) are arranged to show the distribution in relation to salinity expressed as density. Certain general features are obvious. Such saline waters are extremely favourable to the growth of Diatoms. In most cases, especially in shallow water, they formed a dense green carpet on the surface of the mud, from which bubbles of oxygen rose during the day. Diatoms were also found alive in water of density 1109 (Station 7). They were recorded too from the mud surface in the saline pan (19) derived from the overflow from Lac Merdjadja (18), the density of the lower water being 1172. Unfortunately these were not examined before preservation, and they may have been washed in from 18 and killed by the sudden increase of salinity and thereby preserved. For reasons of space the records from the two most saline waters (7 and 19) are not included in text-fig. 2.

The complete absence of Myxophyceae and Mollusca from the saline waters of the Oran district (1 to 7) is very striking ; but there was no obvious peculiarity in the composition of these waters as compared with those of the desert where Myxophyceae and Mollusca were widespread (Tables II and IV) and temperature conditions were not peculiar (Table I). Equally remarkable was the absence of Myxophyceae and Diatoms from ' Fontaine Chaude ' (9), a warm spring (23° C.) near Batna. The mud, but not the water, smelt strongly of H_2S, and conditions were just those which might be expected to favour an abundant growth of Myxophyceae. Instead, the flora was composed of masses of *Spirogyra* (2 spp.).

We were unable to find any fauna or flora in the water or bottom mud of Lac Morselli (1), except for some Phyllopod nauplii (sp. undet.). In December 1925 Gauthier (1928, p. 360) found an abundant fauna in this lake, comprising (Phyllopoda) *Branchinella media* and *Branchinectella salina*, (Cladocera) *Moina salinarum* and *Daphnia magna*, (Copepoda) *Wolterstorffia blanchardi* (*Cletocamptus retrogressus*), (Ostracoda) *Eucypris inflata*, and some Ephydrid larvae. It appears, therefore, that the fauna and flora of the lake were, at the time of our visit, in the trough of a depression, the cause of which is quite inexplicable.


SEA-WATER
Density... 1000
1010
1020
1030
1040
1050
1060
1070
Chlorophyceae:
Chaetoceras, sp. undet.
Other Diatoms, spp. undet.
Chlamydomonadales, spp. undet.
Spirogyra, spp. undet.
Vaucheria Thuretii
„ spp. undet.
Cladophora fracta
„ spp. undet.
Rhizoclonium riparium
Enteromorpha intestinalis
Myxophyceae:
Gomphosphaeria aponina
Merismopedia punctata
Coelosphaerium Nägelianum
„ Kützingianum
„ spp. undet
Chroococcus minutus
„ spp. undet.
Cyanothrix Willei
Spirulina subsalsa
Oscillatoria tenuis
„ Cortiana
„ Okeni
„ nigro-viridis
„ formosa
„ terebriformis
„ acutissima
„ spp. undet.
Phormidium tenue
„ molle
„ Corium
Lyngbya aestuarii
„ nigra
„ Martensiana
„ major
Microcoleus chthonoplastes
Schizothrix lardacea
Glococapsa, sp. undet.
Stigonema, sp. undet.
Synechocystis aquatilis
Rotifera:
Brachionus plicatilis
Pedalia fennica
Synchaeta ? tavina
Euchlanis ? proxima
Pleurotrocha petromyzon
Monocerca lamellata
Notolca scapha
Lecane ? aeganea
„ luna
Rhabdocoelida:
Macrostomum, sp. undet.
Spp. undet.


PHYLLOPODA :
Branchinectella salina
Artemia salina
CLADOCERA :
Daphnia magna
,, atkinsoni
,, ? pulex
Diaphanosoma brachyurum
Simosa exspinosa
Moina salinarum
Alona rectangula
,, ? tenuicaudis
Macrothrix hirsuticornis
OSTRACODA :
Spp. undet.
COPEPODA :
Arctodiaptomus salinus
Cletocamptus retrogressus
Metacyclops minutus
Paracyclops fimbriatus
Echinocamptus vidua
Nitocra lacustris
Horsiella brevicornis
Laophonte mohammed
Megacyclops ? viridis
INSECTA (larvae) :
Aedes detritus
,, caspius
Culex tipuliformis
,, laticinctus
Theobaldia longiareolata
,, annulata
Anopheles multicolor
Ephydra macellaria
Chironomidae, spp. undet.
HYDRACHNIDA :
Eylais megalostoma
Eupatra semiperforata
Arrenurus pervius
NEMATODA :
Spp. undet.
MOLLUSCA :
Hydrobia brondeli
,, ? arenaria
Ammicola pycnocheila
,, letournauxiana
Melanopsis ? maroccana
Melanoides tuberculata
Physa ? myosotis
Pisidium, sp. undet.
PISCES :
Cyprinodon fasciatus
AMPHIBIA :
Rana ridibunda
DENSITY ...
1000
1010
1020
1030
1040
1050
1060
1070

Desert wells (33*a*, 45, 50, 52, 53, 54).

The water in a well is naturally unlikely to be concentrated by evaporation unless the water surface is close to ground level. The most saline of these six wells was Hassi Ali ben Salah (53, density 1010), in which the water surface was only 2 m. down (see Table I). It also had an unusually wide opening (diam. 2·5 m.): the others were about 1 m. in diameter. The complete absence of plant life from all except 53, in which a few Diatoms were found, was obviously due to insufficient light. The fauna of these wells was composed mainly of Cladocera, Copepoda and Nematoda. There were also some Hydrachnida and Chironomid larvae in 33*a* and a few Ostracoda in 53. Hassi Butana (54) contained no organisms of any description. Its water was very similar in salinity and composition to that of 33*a* (see Table II, which also gives an analysis of 52). The only obvious peculiarities of the water in 54 were a slight cloudiness and an unpleasant odour, and the bottom was muddy. In all the others the water was clear and the bottom was of clean sand.

Salinity and distribution.

We have already seen that total salinity is probably the predominant chemical factor. But the fauna and flora must be influenced not only by the actual salinity at a given time, but also by the variations which the same water will undergo from time to time, and which are often obviously extremely large. Colonization of such an environment must therefore entail adaptation to a great range of conditions. It is thus not surprising that inland saline water organisms are of predominantly freshwater and not of marine origin. Life in fresh waters already entails a much higher degree of osmotic independence and of adaptability to changing conditions than is normally required of marine organisms. Moreover, resistant stages are, for obvious reasons, essential for survival in most of these waters, which are liable to complete drought. Such stages, usually in the egg, have been evolved for tiding over unfavourable conditions (including drought) in fresh waters, and are rare with marine organisms.

In studying text-fig. 2, in which the salinity ranges are recorded, it must be borne in mind that very few waters were found with densities between 1030 and 1050. Some of the species whose upper limit is shown at about 1030 would most probably have been found in water of higher salinity than this.

If attention is confined to identified species, it will be seen that those which were found in the most saline waters (above 1050) were those which also had the widest range. Such were *Spirulina subsalsa*, *Schizothrix lardacea*, *Arctodiaptomus salinus*, *Cletocamptus retrogressus*, *Nitocra lacustris*, *Megacyclops ? viridis*, *Aedes detritus* and *Ephydra macellaria*. It is only to be expected that if an organism possesses an osmo-regulatory mechanism sufficiently effective for life in very high salinities, it should be able to live in much more dilute water so long as this is hypertonic to the body fluids. In none of the above species is the concentration of the body fluids known with the exception of *Aedes detritus*. Under experimental conditions this larva can live indefinitely and pupate in fresh water, though there are no records of its occurring naturally in any but definitely saline waters. When the salinity of the medium is below about 0·8 per cent (density *c.* 1005) the blood is maintained hypertonic to the medium; in water more saline than this it is hypotonic (Beadle, 1939). It may be that its absence from fresh waters is due to the necessity for a high salinity for the hatching and development of the eggs—a point which might be settled by experiment. In any case, this example serves as a warning that the natural salinity range of a given stage in the life-history of a species may be much less than the actual tolerance range, and may be restricted by the tolerance of some other stage. *Artemia salina* should also be included in this group of species, though its range as shown in text-fig. 2 is very narrow. Gauthier (1928, p. 370) found it in water with a density as low as 1017, and Medewewa (1927) recorded it from a salinity range of 2–22° Baumé (*c.* 1012–1134).

There were several species which had an intermediate salinity range, not being recorded from very dilute or very saline water. Such were *Vaucheria thureti*, *Synchaeta ? tavina*, *Branchinectella salina*, *Daphnia atkinsoni*, *Aedes caspius*, *Hydrobia brondeli* and *Cyprinodon fasciatus*. The remainder were confined to waters of density less than 1010, the range of many of these extending into fresh water. The majority of this group have been recorded elsewhere from fresh water, and it is obvious that they, and some at least of the intermediate group (e.g. *Daphnia atkinsoni*), are primarily freshwater organisms with varying degrees of resistance to low salinities.

So far as osmotic regulation is concerned, organisms capable of life in saline water are probably of three types :—

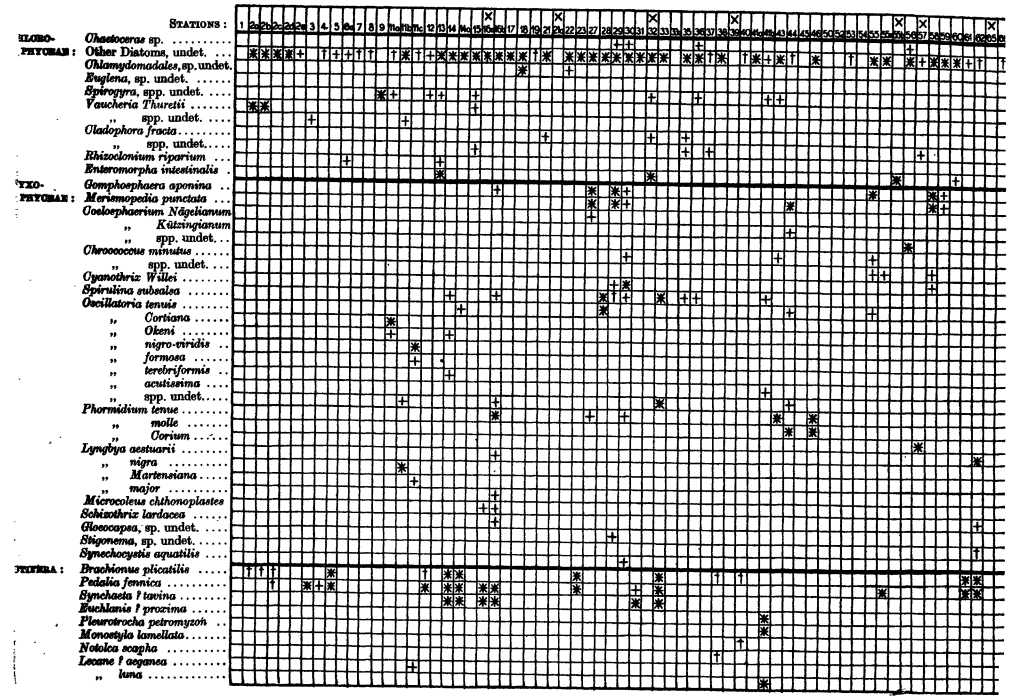
(i) Most freshwater forms which can maintain a hypertonic internal medium in fresh water, but are unable to prevent an increase of internal concentration in saline water. These can withstand a certain degree of salinity, but a limit is set by the maximum body fluid concentration which can be tolerated. This maximum depends upon the normal concentration maintained in fresh water, and varies with different species (Beadle and Cragg, 1940). The maximum external salinity tolerated by most purely freshwater species is probably equivalent to about 20 to 40 per cent sea-water (density 1004–1009) (Beadle and Cragg, 1940). Those species reported here from densities less than 1010, together with some from intermediate densities, are almost certainly of this type.

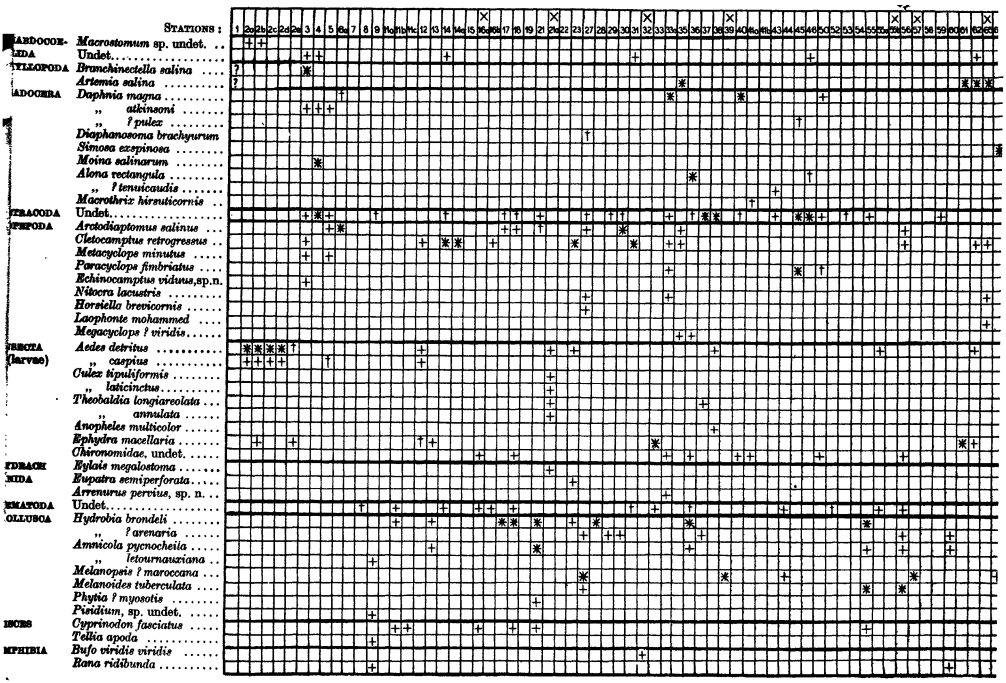
(ii) Most marine organisms whose body fluids when in sea-water are practically isotonic with the medium, and whose tissues are adapted to this concentration. These possess no means of regulating their body fluid concentration, and the salinity tolerance range is thus limited. The coastal brackish water organisms are mainly derived from this type and have evolved a mechanism for maintaining hypertonic body fluids in dilute sea-water, a line of evolution which ultimately leads to the freshwater type. Both marine and coastal brackish water organisms have been reported from the inland saline waters of North Africa—e.g. Foraminifera (Gauthier-Lièvre, 1935), *Chaetoceras* sp., *Enteromorpha intestinalis* (Gauthier-Lièvre, 1935) and *Palaemonetes varians* (Gurney, 1909); but, as might be expected, they have not been found in waters of much greater salinity than sea-water, and the mechanism for maintaining hypotonic body fluids and protoplasm in very saline media has probably not been adequately developed.

(iii) Those organisms which have a powerful mechanism for maintaining hypotonic body fluids and are thus able to prevent undue rise of internal concentration in very saline water. From morphological considerations it is obvious that these truly saline water forms are derived from freshwater types, and this is supported on physiological grounds by the work of Medewewa (1927) on *Artemia salina* and of Beadle (1939) on *Aedes detritus*, who showed that the blood concentration maintained by these animals is characteristic of purely freshwater animals. Those organisms recorded here from densities greater than 1050 must be of this type. Some of those from intermediate salinities would probably also be included if their osmo-regulatory mechanism could be investigated. Some of these inland salt-water forms are also found in the sea and coastal brackish water, e.g. *Brachionus plicatilis*, *Synchaeta ? tavina* and *Aedes detritus*. But they are not properly marine in the sense defined above, and have been evolved from freshwater ancestors.

Other possible factors.

It has been assumed that the efficiency of the osmoregulatory mechanism in relation to the external salinity is the chief factor which determines the occurrence and distribution of organisms in these waters. The analyses in Table II do, in fact, suggest that total salinity is the most important variable likely to affect the nature of the fauna and flora. But it must be admitted that there are several other factors





\+ Recorded.
* Particularly abundant.
† Very rare.
? Phyllopod nauplii only found.

× Collections at these stations were not complete, organisms other than those recorded may have been present.
A key to the stations is given in Table I.

which may reduce the actual range of a species within the limits set by salinity. The following are some possibilities :—

Hydrogen ion concentration. The range of the *p*H values recorded (Table I) was relatively small and on the alkaline side of neutrality (7·5–9·1). The high alkalinity figures suggest that the waters were well buffered and thus unlikely to undergo large diurnal *p*H fluctuations due to photosynthesis. A good demonstration of the degree of buffering was given by the water coming from the main artesian boring at Touggouert (57). This at the source was saturated with CO_2 and slightly effervescing. The *p*H, originally 7·5, rose after thorough shaking to a maximum of 8·1. These are very close to the figures got from sea-water saturated with CO_2 and in equilibrium with air respectively (Harvey, 1928, p. 70). This correspondence would be expected on theoretical grounds, since the alkalinities of both are nearly equal (57, 0·0023, sea-water 0·0026 N), and the *p*H/CO_2 tension curves should therefore follow the same course. The divergence due to difference in total concentration of cations, as calculated from Saunders' equation, would be insignificant (Saunders, 1926).

The two pools (2*a*) and (2*b*) close to Lac Morselli between 08.00 and 11.30 hours on a cloudless day showed *p*H changes of 7·5–7·7 and 8·3–8·4 respectively. Both of these contained an abundant growth of *Vaucheria Thuretii*. The *p*H of the desert pool, Square Bresson (33), changed from 8·5 to 8·7 between 07.00 and 14.00 hours. In this the Diatom flora was very rich. It therefore seems improbable that *p*H fluctuation is a factor of much importance in determining the nature of the fauna and flora.

Dissolved oxygen. Reasons have already been given for assuming that oxygen is never likely to be reduced sufficiently to affect the respiration of aerobic organisms (p. 48).

Sulphuretted hydrogen. The frequent occurrence of H_2S in these waters has already been discussed. That it should act as a limiting factor is probable. Some at least of the animals and plants seem to be unaffected by its presence (e.g Stations 28 and 33), and it is well known that several blue-green algae, especially Oscillatoriaciae, are common in the waters of sulphur springs.

Nutrient salts. No estimations were made of phosphate, nitrate or silicate; but owing to the general great abundance of plant life, including Diatoms, it is probable that the supply of these salts is never short, at least in winter, when our collections were made. It is, of course, possible that later in the season they may become exhausted in some of the stagnant waters ; but these are unlikely to escape complete evaporation in the summer, unless they are periodically renewed by irrigation water, which would supply more nutrient salts.

Light. There is certainly no likelihood of insufficient illumination for plant life ; but it is very probable that in the desert summer the light would be too intense for some organisms, and photosynthesis in shallow waters might be completely inhibited.

Temperature. With the exception of Hammam es Salahine (11), where typical hot spring conditions prevail, most of the water temperature records taken at various times of day range between 8° C. and 26° C. (Table I). The average minimum shade temperature during our stay at Touggouert in February was 3·3°, and a slight frost at dawn is normally recorded more than once during every winter from most of the meteorological stations in the Northern Sahara. On such occasions very shallow and exposed waters may become coated with a thin film of ice (Gautier, 1928). It is therefore probable that organisms in shallow pools are unable to escape temperatures below 5° C. on several occasions during the winter, though they would never become completely frozen. How far fluctuations within these limits are likely to regulate the nature of the fauna and flora cannot be known without further observation and experiment. The scarcity of cichlid fish in the upper layers of the Oued Rhir lakes during the winter might reasonably be ascribed to low tem-

perature. That much higher temperatures may be reached in other than thermal waters under special conditions is shown by the case of 19 (discussed on p. 228). It is certain that the temperature (31° C.) of the lower water of 19 is sufficiently high to restrict the fauna and flora to forms with special thermal adaptations, though in this case the extremely high salinity is also a limiting factor. In summer, when shade temperatures may exceed 40° C., there is no doubt that the organisms in shallow and exposed waters must be affected. It would therefore be interesting to observe the changes at the onset of the hot season and to correlate these with experiments on the effects of high temperatures upon various species.

The many natural and artificial up-wellings of water with a constant temperature between 20° and 26° C. in the Oued Rhir might be expected to afford a temporary asylum for organisms unable to withstand the high summer temperatures in shallow waters ; but at least some of the organisms recorded here from other than thermal waters are capable of adaptation to high temperatures. The fish *Cyprinodon fasciatus* is an outstanding example. It was caught in water at 9° C. (16*a*) as well as in the stream (35° C.) flowing from the hot spring at Hammam es Salahine (11*c*). It had previously been recorded closer to this spring in water at 40° C. (Pellegrin, 1921, p. 35). *Rana ridibunda*, recorded here at 23° C. (9) and 24·5° C. (60), was found by Mason (1939) living permanently at 38° C., and temporarily, at even higher temperatures (up to 41° C.), at Hammam Meskoutine in N. Algeria. Many of the Myxophyceae in Table IV have been found elsewhere in hot springs—*Oscillatoria Cortiana, O. Okeni, O. formosa, O. terebriformis, O. tenuis, Spirulina subsalsa, Schizothrix lardacea, Lyngbya nigra, L. Martensiana, Merismopedia punctata* (Geitler, 1932 ; Gauthier-Lièvre, 1931) and *Lyngbya aestuarii* (Mason, 1939).

A characteristic feature of desert temperature conditions, apart from seasonal extremes, is the relatively enormous diurnal fluctuation at all seasons. The average amplitude (max.–min.) of the diurnal fluctuation of shade temperature at Touggouert is about 13° in winter and 17° C. in summer. Farther south, at Adrar, the corresponding figures are 17° and 24° C. (Lasserre, 1922). Fluctuations on many individual days will be much greater than the average (e.g. 20° C. at Touggouert on 3. 3. 38), and the fluctuation amplitude of unshaded air temperature would, of course, be very much larger. It is therefore necessary for organisms living in exposed shallow waters to be well adapted to large and rapid temperature changes. This would also form an interesting subject for experiment.

Additional notes on the fauna and flora.

These are not intended to be exhaustive, but comprise a few extra points of interest relating mainly to previous records of some of the recorded organisms.

Chlorophyceae.

Chaetoceras sp. This is a well-known marine pelagic genus, very rarely recorded from inland waters (Thienemann, 1925). It was found by Gauthier-Lièvre, but not by us, in Lac Temacine (17). We found it in four localities in the Oued Rhir (water density 1004–1008).

Enteromorpha intestinalis Link. A marine and estuarine alga previously reported from irrigation channels in the Algerian and Tunisian deserts (Gauthier-Lièvre, 1931).

Myxophyceae.

Cyanothrix Willei Gardner. According to Geitler (1932) this has been recorded previously only from standing water in Porto Rico, Central America (salinity not mentioned). It was found by us in three slightly saline waters (density 1005–1007) and has been identified by Dr. K. B. Blackburn in Prof. Omer Cooper's saline water collections from Siwa Oasis in the Egyptian Desert (personal communication).

Merismopedia punctata Meyen. Not mentioned by Gauthier-Lièvre (1931) as having previously been recorded from N. Africa, though found by us in six saline waters of the Oued Rhir. Recorded elsewhere from saline and thermal waters (Geitler, 1932).

Phormidium molle Gom. Also not recorded by Gauthier-Lièvre (1931), though known elsewhere from inland saline waters (Geitler, 1932).

The remainder of the identified Myxophyceae have previously been recorded from N. African saline waters (Gauthier-Lièvre, 1931).

ROTIFERA.

Brachionus plicatilis Müller (*B. mülleri* Ehrbg.). A very well known estuarine and coastal salt marsh species. It has also been recorded from inland saline waters in Europe and East and South Africa (Thienemann, 1931 ; de Beauchamp, 1932 ; Hutchinson *et al.*, 1932).

Pedalia fennica Lev. I am indebted for the following information to Dr. J. Wiszniewski, to whom some of my samples were sent by Prof. de Beauchamp. Many varieties of the species *fennica* are recognized, of which *bulgarica* and *jenkinae* are extremes. This Saharan form is perhaps another variation characterized by a tendency to reduction in the number of hairs on the locomotory appendages.

It has been found in neutral and alkaline saline waters in South Africa (Hutchinson *et al.*, 1932) and rarely in saline acid waters (e.g. in Central America : Juday, 1916). Reported once from North Africa in Gauthier's collection from L. Fetzara on the north coast of Algeria (de Beauchamp, 1930). Gauthier (1928) indicates that the water was saline, but no figures are given. It was the most abundant of the Rotifers in our collections, especially in moderately high salinities. In some cases (e.g. 33 and 36) they were numerous enough to make the water cloudy.

Synchaeta ? *tavina* Hood. Prof. de Beauchamp writes : " Probablement *Synchaeta tavina* Hood, malgré de légères différences : cette espèce n'était connue que de la Mer du Nord, et s'il y a nombreuse *Synchaeta* d'eau saumâtre au bord de la Mer, elles paraissent exceptionnelles dans les lacs salés interieurs."

B. plicatilis and *P. fennica* were usually found together, and *S.* ? *tavina* was never found unaccompanied by *P. fennica*.

Monostyla lamellata Daday. Also found in Gauthier's collection from L. Fetzara, N. Algeria (de Beauchamp, 1930). Otherwise known from alkaline saline lakes in Eastern Europe and North and Central America (Harring and Meyers, 1926).

Notolca scapha Gosse (*N. striata* Müller). Well known marine and estuarine species, recorded from German inland saline waters (Westfalen) by Thienemann (1913).

The remaining Rotifers, with the exception of *Lecane* ? *aeganea*, whose identification is uncertain, were all found in the freshwater lake (41 *b*) at El Golea. They are known only from fresh waters.

PHYLLOPODA.

Branchinectella salina Daday. So far found only in saline waters of French North Africa. Gauthier (1928) records it from waters of density range 1010–1030. We found it only in the Sebkha d'Oran (3 : density 1016).

CLADOCERA.

Daphnia magna Strauss, *Moina salinarum* Gurney, *Alona rectangula* Sars, and *Simosa exspinosa* de Geer have all been previously recorded from coastal and inland saline waters of Algeria (Gauthier, 1928). Of these it seems that *M. salinarum* is the only exclusively saline species.

Daphnia atkinsoni Baird. Found by Gauthier (1928) only in fresh water, but Gurney (1909) found it in the salt lake Sedjoumi near Tunis.

Diaphanosoma brachyurum Liévin. Previously found in North Africa in fresh water only (Gauthier, 1928).

COPEPODA.

These were identified by Dr. F. Kiefer, whose report is as yet unpublished. The synonyms given in brackets are those used by Gauthier (1928).

Arctodiaptomus salinus Daday (*Diaptomus salinus* Daday) and *Cletocamptus retrogressus* Schmank (*Wolterstorffia blanchardi* Richard). The salinity range for these two species recorded by Gauthier (1928) was close to that given in text-fig. 2, but he also found them in fresh water.

Metacyclops minutus Claus (*Cyclops minutus* Claus). Recorded by Gauthier (1928) from a number of localities in French North Africa, but none of these was apparently saline; but the *Cyclops diaphanus* Fischer found by Gurney (1909) in water of density 1007 in Sebkha Sedjoumi in Tunisia is considered by Gauthier to be the same species.

Paracyclops fimbriatus Fischer (*Cyclops fimbriatus* Fischer). Found in three desert wells, two of which (45 and 50) were fresh and the third slightly saline (33 *a* : density 1007). Gauthier (1928) records it only from running fresh waters in Northern Algeria and Tunisia.

Megacyclops ? viridis Jur. (*Cyclops viridis* Jur.). If this is indeed the same species recorded by Gauthier from a large number of fresh waters in Northern Algeria and Tunisia, and once only from slightly saline water in the Marais de la Macta near Oran (density 1002 max.), it is interesting to note that we found it in the extremely saline Ouargla Chott (density 1054) and in a stream running into it (density 1008).

Echinocamptus (*Limocamptus*) *viduus*, sp. n. This new species is described by Kiefer from two females taken in the Sebkha d'Oran (3 : density 1016).

INSECTA.

The mosquito larvae *Aedes detritus* Edw. and *A. caspius* Pallas are well known inhabitants of saline waters, to which they seem to be confined. They both possess the extremely reduced anal gills characteristic of saline water forms (Beadle, 1939). The remaining mosquito larvae are normally found in fresh, but have all on occasions been recorded from slightly saline waters.

SUMMARY.

(1) An expedition to study the ecology of some inland saline waters in Algeria was undertaken in the winter (January to March) of 1938. Some 60 waters were examined, seven near Oran on the north coast, and the remainder in the Oued Rhir district of the northern Algerian Sahara.

(2) The origin of these waters is briefly described.

(3) The range of water densities found was 1000–1172 (fresh water 1000, sea-water 1022); *p*H 7·5–9·2; alkalinity 0·0010–0·0190 N.

(4) Total analyses of representative samples show that they are of the sulphato-chloride type, being 'physiologically' well balanced, but containing relatively less Cl and more SO_4 than sea-water.

(5) The relative ionic composition is altered with increasing concentration, due mainly to precipitation of Ca and SO_4; but it seems that such changes are unimportant, compared with differences in total salinity, in determining the nature of the fauna and flora.

(6) A comparison of the salinity ranges of the identified organisms suggests that they fall into three main groups: (i) freshwater species with capacity for adaptation to low salinities; (ii) forms found only in intermediate salinities; and (iii) those capable of living in extremely saline water. This last group has also the greatest salinity range.

(7) The few marine types present (e.g. the Diatom *Chaetoceras* sp. and the alga *Enteromorpha intestinalis*) are found only in relatively low salinities. The majority are of freshwater origin, including those adapted to the most saline waters. These facts are discussed in relation to experimental work on osmotic regulation.

(8) A curious condition of water layering was found to be fairly common. A warm, sometimes very hot, layer of saline water is overlaid by a cooler and less saline layer. In one case (19), where the total depth was only 0·3 m., the density of the lower water was five times that of the upper. In such cases the lower stagnant layer may contain simultaneously both H_2S, due to reduction in the mud, and O_2 in high concentrations as the result of Diatom photosynthesis in the water.

(9) High salinity and illumination favour an abundant growth of phytoplankton, especially Diatoms. It is concluded that exposed waters in deserts are probably always well oxygenated, reduction being more than compensated by photosynthetic oxygen production.

(10) Other factors of possible biological importance, such as temperature, are also discussed.

(11) A few observations were also made on thermal waters and desert wells.

(12) As the result of this work several problems requiring more thorough investigation are suggested.

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7 MAY 1946

The seasons in a tropical rain-forest. Part 6. Lizards (*Emoia*).

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(With 1 Text-figure)

[Read 7 June 1945]

Introduction.—In previous papers in this series, the breeding seasons of mammals and birds in the island of Espiritu Santo, New Hebrides (Pacific Ocean), have been considered. It may be recollected that Hog Harbour, where the investigation was made, was chosen on account of the remarkably uniform climate. Although more rain falls at one time of year than at another, yet there is no dry season. Temperature changes are very small. The site is 15° 15′ south of the equator. There are few places on the surface of the earth where seasonal changes in meteorological conditions are smaller. It was thought interesting to find out whether animals respond to the conditions by breeding all the year round. The chosen mammals and birds were found to have restricted breeding seasons. The present paper is concerned with the reproduction of two species of lizards.

On his second visit to the New Hebrides, in 1927, the writer studied the reproduction of one of the lizards considered in this paper (*Emoia werneri*), and published a brief account of it (Baker, 1929). In 1933–4 he visited the islands again with the expedition made under the auspices of the Oxford University Exploration Club. The expedition had the financial support of the Royal Society, the Percy Sladen Memorial Fund, the University of Oxford and of New College, Oxford. The writer wishes to acknowledge the help rendered by the other members of the expedition (Miss I. Baker, Mr. T. F. Bird, Mrs. Z. Baker, Mr. T. H. Harrisson and Mr. A. J. Marshall) in the weighing, dissection and preservation of specimens of *Emoia cyanura*. Mr. H. W. Parker kindly indentified our reptiles and gave information about them.

Description of the species investigated.—Fourteen species of lizards occur in the New Hebrides, all belonging to the widely distributed families of skinks and geckoes. The most abundant of all are the little skinks, *Emoia cyanura* (Lesson) and *E. werneri* (Vogt). These are the two species with which this paper deals. They were chosen on account of the ease with which large numbers could be obtained throughout the year. They are especially abundant in native villages and clearings, where they expose themselves freely to the sunshine. They are agile, and the limbs are not nearly so much reduced as they often are among the skinks.

Emoia cyanura (=*Lygosoma cyanurum*). Among 622 specimens weighing 1·5 gm. and over, the two largest (both males) weighed 3·3 gm. There is a longitudinal golden stripe running right down the back and another parallel to it on each side. The space between the golden stripes is brown or brownish golden. The tail is dull olive green during life. In preserved specimens its colour sometimes changes to a blue resembling that of *E. werneri*. It is unfortunate that the name cyanura should refer to a species in which the tail is in life so far from Κυανεος (glossy blue).

E. werneri (=*Lygosoma kordoanum*=*Lygosoma lessoni*). The two largest specimens each weighed only 2·4 gm. This is a far more brilliantly coloured species than *E. cyanura*. There are the same three longitudinal golden stripes, but the spaces between them are almost black, while the tail is a brilliant powder blue. (This colour begins behind the hind legs, while the olive green of *E. cyanura* begins further

forward.) A very good likeness of this species, in colour, is given by Duperrey (1826), though the picture is stated to refer to *Scincus cyanurus*. For the anatomical distinction between *E. cyanura* and *E. werneri*, see Parker (1925). The two species were formerly confused under the name of *Lygosoma cyanurum* (see Boulenger, 1887).

The young of both species have the same colour as adults, and there is no sexual difference.

The specimens used in this investigation were caught by native children in return for rewards.

The reproductive cycle in the female.—Emoia cyanura. This is the species studied by the 1933–4 expedition. It will be taken first because it was investigated more thoroughly than the other species.

Specimens were collected in the middle of each month of the year from September 1933 to August 1934, inclusive. It was found that no sudden change occurred in the reproductive condition, and the data are therefore grouped together in bi-monthly periods in the analysis (September-October, November-December, etc.).

In any study of breeding seasons, it is of prime importance to fix the criteria by which adults can be distinguished from young. In *Emoia* the criterion of body-weight is adequate. No female weighing (with intact tail) 1·5 gm. or less was found to have eggs in the oviduct, while eggs were found in the oviducts of specimens in each 1/10 gm. weight-group from 1·6 gm. upwards. Females weighing 1·6 gm. and over were therefore regarded as adult.

On dissection, it is immediately apparent whether there are eggs in the oviducts, as the eggs are quite large (about 0·2 gm. each). Specimens with eggs in the oviducts are called *ovigerous*. In these specimens there is almost always one egg in each oviduct. Large Graafian follicles are not found in the ovaries of ovigerous females, but each ovary contains a rather irregularly-shaped body resembling a corpus luteum.

In specimens that were not ovigerous, the diameter of the largest follicle in the ovaries was measured, in order to provide a criterion of fecundity. If the largest follicle was 3·0 mm. or more in diameter, the specimen was regarded as fecund; if less, as non-fecund. The figure of 3·0 mm. serves well to distinguish between the many specimens with inactive ovaries containing no follicle measuring more than 1·5 mm., and those others, in full reproductive condition, with follicles up to 6 mm. across, or occasionally even more (7·5 mm.). Few specimens have follicles of intermediate size (about 2 or 2·5 mm.). The size of the growing oocyte is approximately the same as that of the follicle, for the wall is thin.

Adult females, then, are classified as ovigerous, fecund, or non-fecund. Those in the two former categories are described as being in a reproductive state.

The average number of adult females dissected in each bi-monthly period was forty-four. The percentage of adult females that were in a reproductive state in each such period is shown in fig. 1 and Appendix I. 60 % were reproductive in November–December, and the figure falls smoothly to reach a minimum (15%) in May–June. In no single month in the year is reproduction at a standstill, though only one ovigerous female was found in June. A peculiar point is that the two ovigerous females taken in May each contained only one egg, instead of the nearly invariable two.

Many young specimens, weighing 1·5 gm. or less were collected in each bi-monthly period of the year.

Emoia werneri. This species was studied by the writer in 1927. Natives continued the collection and preservation of specimens after he had returned to England, under the supervision of the Rev. W. Anderson, and thus the whole year was covered. A brief report has been published (Baker, 1929), but too low a weight was selected as a criterion for adults, and re-analysis is therefore necessary.

Female *E. werneri* are in this paper regarded as adult if they have attained a weight of 1·25 gm. or more. The reproductive condition of adults in each bi-monthly

period is shown in Appendix I. The same criterion of fecundity was used as in the work on *E. cyanura*. The number of specimens studied was smaller than of the other species (136 adult females instead of 266).

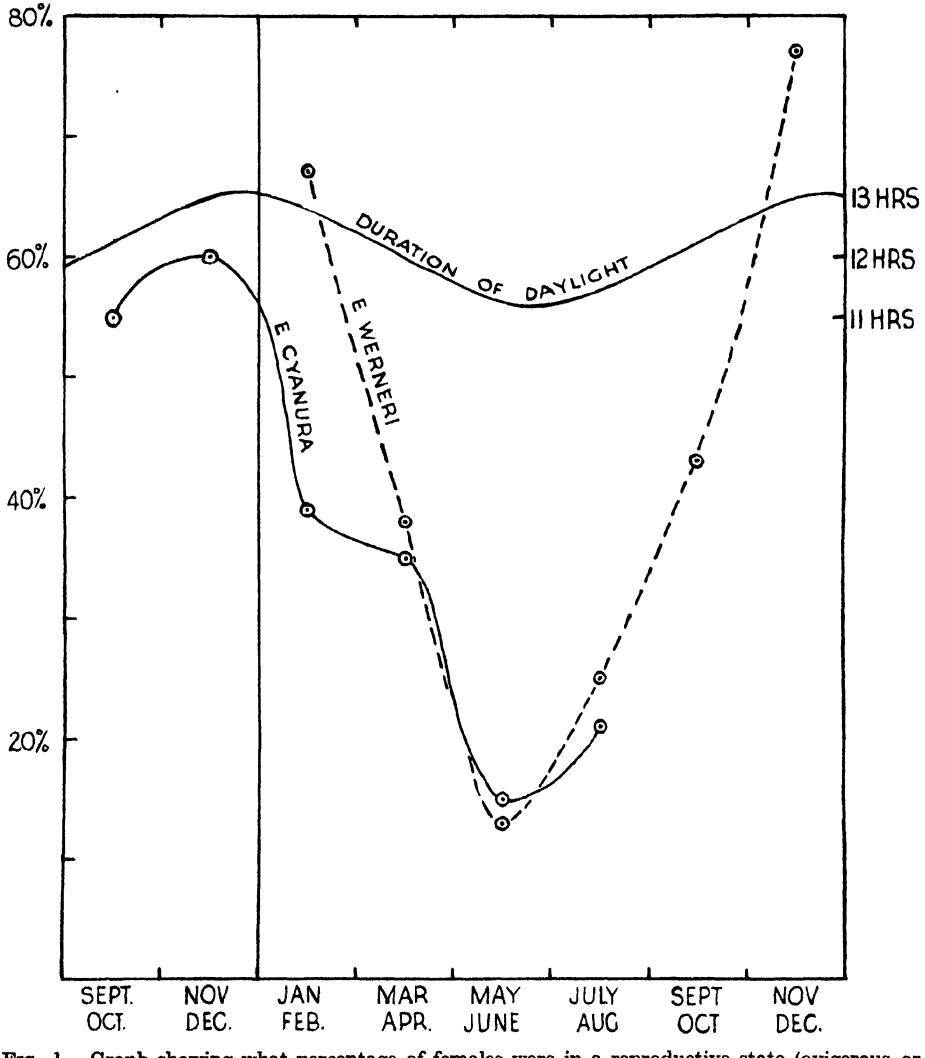

FIG. 1.—Graph showing what percentage of females were in a reproductive state (ovigerous or fecund) in each two-monthly period. The curve at the top of the graph shows the seasonal change in duration of daylight.

Fig. 1 shows that the percentage of adult females that were in a reproductive state in each bi-monthly period of the year corresponds well with the data for *E. cyanura*. As in that species, the figure reaches its highest point in November–December and its lowest in May–June. No ovigerous female was collected in May,

but since only eight adult females were dissected in that month, this cannot be taken to prove that reproduction was actually at a standstill at that particular time. However, none of the twenty-seven non-ovigerous females collected in May–June was fecund, and it is therefore clear that reproduction was at a low ebb at that season.

Many young specimens, weighing 1·25 gm. or less, were collected in each bi-monthly period of the year.

The reproductive cycle in the male.—E. cyanura. Males weighing 1·5 gm. and over were regarded as adult. The average number of adult males dissected in each bi-monthly period was forty-two. The testes of adult males were preserved in formol-salt-alcohol and weighed after preservation. All the testes collected during one month were put on the balance together, so as to minimize loss of weight by evaporation during weighing. The bi-monthly data are given in Appendix 2. Preservation causes a small loss of weight, and the figures given are somewhat less than they would have been if the organs had been weighed in a fresh condition.

The mean weight of the testes was high (about 22 mg.) from September–October till January–February and then fell off, reaching its lowest point (8 mg.) in May–June, when the reproductive processes of the female were also at their minimum.

The diameter of the seminiferous tubules, measured in microscopical sections, was about 250μ in November and had sunk to about 180μ in May–June. There was thus nothing approaching the marked change that occurs in the Passerine bird, Pachycephala, in the same locality (Baker, Marshall and Harrisson, 1939).

E. werneri. Males weighing 1·25 gm. and over were regarded as adult. The average number of adult males dissected in each bi-monthly period was seventeen, and the fewest in any such period eight. Spermatozoa were seen in the epididymis of every adult male except five, and were abundant in the great majority throughout the year. At the reproductive minimum, in May–June, spermatozoa were present at full abundance in sixteen out of the nineteen adults examined, and in reduced numbers in the other three. It is thus clear that males remain in reproductive condition throughout the year.

Remarks.—Since each of the studies reported in this paper lasted only twelve months, there is no conclusive proof that the cycle in reproduction is annual; but the fact that the data for 1927 (*E. werneri*) correspond closely with those for 1933–4 (*E. cyanura*) suggests strongly that the cycle is in fact annual in both species.

The minimum of reproduction in both species corresponds with the period of shortest days and the maximum comes when the days are nearing their longest (fig. 1). The longest day is 1 hour 48 minutes longer than the shortest.

This paper concludes the detailed accounts of the seasonal reproductive phenomena shown by the selected terrestrial vertebrates at Hog Harbour, New Hebrides. It remains only to bring together the general conclusions that can be derived from the data presented in this and the five previous papers in the series. It is hoped to publish the general conclusions in a final paper.

Summary.—(1) This paper is concerned with the reproduction of two species of skinks in the remarkably unvarying tropical climate of Hog Harbour, Espiritu Santo, New Hebrides (15° 15′ S., in the Pacific Ocean).

(2) The reproductive cycle of each species was studied over a period of twelve months, *Emoia werneri* in 1927 and *E. cyanura* in 1933–4.

(3) In both species reproduction was at its height in November–December and at its lowest ebb in May–June. *E. cyanura* produced eggs throughout the year, but *E. werneri* appears to have failed to do so in May.

(4) Males in reproductive condition are found in both species throughout the year.

(5) At the time of reproductive minimum (May–June), the testes weigh about one-third as much as at the reproductive maximum (*E. cyanura*).

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APPENDIX I, showing the numbers and percentages of adult females in various reproductive conditions.

	Total number examined	Number ovigerous	Per cent. ovigerous	Non-ovigerous			Per cent. of all adult females in a reproductive state (ovigerous or fecund)
				Total number	Number examined for fecundity	Number fecund	
Emoia cyanura.							
Sept.–Oct.	43	17	40	27	27	7	55
Nov.–Dec.	55	16	29	39	39	17	60
Jan.–Feb.	46	12	26	34	34	6	39
Mar.–Apr.	48	9	19	39	39	8	35
May–June	27	3	11	24	23	1	15
July–Aug.	47	6	13	41	41	4	21
Emoia werneri.							
Jan.–Feb.	9	2	22	7	7	4	67
Mar.–Apr.	50	10	20	40	18	4	38
May–June	31	4	13	27	27	0	13
July–Aug.	12	2	17	10	10	1	25
Sept.–Aug.	21	5	24	16	16	4	43
Nov.–Dec.	13	8	62	5	5	2	77

APPENDIX II, showing the weights (preserved) of the testes of adult male *E. cyanura.*

	Number of pairs of testes weighed	Total weight (milligrams)	Mean weight per pair (milligrams)
Sept.–Oct.	33½	740	22
Nov.–Dec.	35	800	23
Jan.–Feb.	32	675	21
Mar.–Apr.	57	780	14
May–June	44½	340	8
July–Aug.	50½	890	18

The seasons in a tropical rain-forest (New Hebrides). Part 7 (Final part). Summary and general conclusions.

By JOHN R. BAKER, M.A., D.Sc. (Communicated by Prof. E. S. Goodrich, F.R.S., F.L.S.) (From the Department of Zoology and Comparative Anatomy, Oxford.)

(With 1 Text-figure)

[Read 7 June 1945]

Introduction.—In the study of the causes of breeding seasons, physiological investigation alone cannot suffice : it must be reinforced by observations made in natural habitats. It is not sufficient to show experimentally that this or that environmental change will start or stop reproduction in a certain organism : one must try to find what are the causes that start or stop it in nature. In the course of evolution, animals have adapted themselves to respond to certain environmental changes by breeding, and to others by stopping breeding. Breeding seasons can only be understood when these changes are known. It is not necessarily relevant to the problem of breeding seasons to discover what environmental changes can be used artificially to start or stop reproduction. For instance, one may prevent an animal from breeding by depriving it of vitamin E ; but unless lack of this vitamin is the cause of the cessation of breeding in nature, the knowledge gained by the experiment does not throw light on the adaptation of the organism to its environment. In fact, one might almost as well study animal locomotion by propelling the animal mechanically or breaking its legs. These facts have tended to be overlooked, and purely physiological studies have been regarded as throwing direct light on the natural mechanism by which breeding seasons are controlled (see Baker, 1938). Such physiological studies may have great intrinsic interest and practical importance, but may not illuminate the subject of breeding seasons.

One of the most interesting natural habitats in which to investigate the breeding seasons of animals is the tropical rain-forest, for here the environmental conditions vary less during the year than in any other part of the land-surface of the world. A study of the climates of tropical rain-forest regions all over the world shows that the northern New Hebrides (in the western Pacific Ocean) have a particularly unvarying climate. The mean temperature of the hottest month is not much more than 2° C. higher than that of the coolest, and rain falls so abundantly throughout the year that on the average of many years the driest month in the New Hebrides is wetter than the wettest in most parts of England.

The study of the seasons in the rain-forest of the northern New Hebrides was the main object of the Oxford University Expedition, 1933–4. The whole of the expedition's work on this subject was done in the vicinity of Hog Harbour, in the island of Espiritu Santo (15° 15′ S.). The members of the expedition were Mr. T. F. Bird, Mr. A. J. Marshall, Mr. T. H. Harrisson, Mrs. Z. Baker, Miss I. Baker, and the writer. All the members shared the work in the field, which started at the beginning of September 1933 and ended at the beginning of September 1934. The results of the expedition have been recorded in six papers in this journal, which are quoted in the list of references at the end of the present paper. The purpose of this paper is to provide a summary of the results and to draw general conclusions.

The expedition set itself two problems :—

(1) Do the vertebrates of this rain-forest region reproduce continuously, or do they have breeding seasons ?

(2) If there are breeding seasons, can they be correlated with any environmental changes ?

A definite answer was obtained to the first question. It was not found possible to answer the second question positively, but proof was obtained that certain environmental factors do not control certain breeding seasons.

To prove that a species is *not* breeding at a certain time demands intensive study. The existence of breeding seasons has often been claimed because birds' eggs have been found at one time of year and not at another. In any study of the breeding seasons of birds, nests must of course be searched for and recorded, but conclusions must not be based solely on the success or failure of the search. Proof of the existence of breeding cycles can only be established by the dissection and microscopical investigation of a considerable number of individuals in every month of the year. An investigation of this kind is a large undertaking, and only a few species can be studied in such detail; but the results obtained are sure. The species chosen by the expedition for intensive study were the following :—

A large fruit-bat, *Pteropus geddiei*.

An insectivorous bat, *Miniopterus australis*.

A passerine bird, *Pachycephala pectoralis* (Golden Whistler).

A small lizard (skink), *Emoia cyanura*.

The investigation was based on the dissection of 378 *Pteropus geddiei*, 542 *Miniopterus australis*, 319 *Pachycephala pectoralis*, and 520 *Emoia cyanura*.

Less intensive observations were also made on other insectivorous bats and on the smaller fruit-bat, *Pteropus eotinus*. Mr. T. H. Harrisson and Mr. A. J. Marshall also made a general study of the reproduction of birds, which they propose to publish when they are released from military duties.

Observations were also made on the flowering and fruiting of certain common wild plants, namely :—

An orchid, *Corymborchis veratrifolia*.

A fig, *Ficus copiosa*.

Wild Kava, *Piper methysticum*.

A deciduous tree, *Garuga floribunda*.

A large leguminous tree, *Castanospermum australe*.

A rose-apple, *Eugenia Richii*.

A strand-tree, *Barringtonia asiatica*.

A bush (Rubiaceae), *Psychotria aneityensis*.

A small herb, *Geophila herbacea*.

Observations were also made on the plant called by the natives 'nasukonru'. This is probably the commonest angiosperm of the northern New Hebrides. Nearly everywhere it is the dominant plant of the forest undergrowth. Curiously enough, neither flower nor fruit of this species was seen by any member of the expedition throughout the year, except that flower-buds were seen on one occasion in the high mountains, far from the scene of the breeding-season investigation. The natives, who are keen naturalists, state that they do not know the flower of this species, which was doubtfully identified from our leaves as *Procris pedunculata*.

The plants were studied because it was thought that they might provide a sensitive index of meteorological changes.

The animals and plants named in the two lists given above will generally be referred to by their generic names only in this paper, for the sake of brevity.

The meteorological changes during the year were studied in detail. Instruments were exposed both in the standard way and also in the forest itself.

A summary of the seasonal changes in weather and reproduction.

The contents of the six preceeding papers in this series are very briefly summarized below, each month of the year being treated separately. Fig. 1 represents the main facts of the breeding seasons graphically.

September.

When the expedition began its work, the length of day (nearly 12 hours) was increasing; the daily period of sunshine averaged nearly six hours. The heaviest rains had not started, and the mean barometric pressure was higher than in any other month of the year. The temperatures shown by all the thermometers (by the maximum and minimum in the Stevenson screen and the grass-minimum in the open, as well as by the maximum, minimum and earth-thermometers in the forest) were about half-way between the highest and lowest recorded during the year. The temperature was to rise and the rainfall to increase in succeeding months as the length of day increased, and then all were to fall away until they began to rise once more before the year's work was complete. Thus the expedition started work at the end of the southern winter; but it is absurd to apply such a term as winter when the climate was so hot and the annual temperature changes so small, and it is better to say the end of the borepheuge (the period during which the sun has left its most northerly point but is not yet overhead at the equator). The notodune (southern spring) started when the sun reached the equator at the September equinox.

Two of the observed plants showed no change in their reproductive condition throughout the year, and they need therefore only be mentioned once. These are the common undergrowth herb, *Geophila*, which reproduced continuously, and the 'nasukonru', which, as has been stated above, never showed a flower or fruit in any of the twelve months of observation. All the other observed plants except *Corymborchis* were in flower or fruit in September. Early in the month *Garuga* was devoid of leaves. This large leafless tree had a remarkably incongruous appearance when the luxuriantly green rain-forest was viewed from the sea. Later in the month leaves appeared, and with them the flowers, which were not seen again during the year. This is the most obviously seasonal plant in the northern New Hebrides.

A few of the fruit-bats, *Pteropus*, were pregnant, but the main season for reproduction was over and the testes of the males were growing in preparation for the next. The females of the insectivorous bat, *Miniopterus*, became pregnant at the beginning of this month (or possibly at the very end of the preceding month). The epididymides of the males were still crowded with spermatozoa. No eggs of the passerine bird, *Pachycephala*, were found, though the testes of the males were near their maximum size. About half the adults of *Pachycephala* were moulting to some extent. The little lizards, *Emoia*, were breeding rapidly, the males having large testes and many of the females being ovigerous.

October.

In this month, just after the beginning of the notodune or southern spring, there was little change in the weather. *Corymborchis* came into flower and all the other plants under observation remained in flower or fruit *. A few females of *Pteropus* were still pregnant, and the testes of the males continued to grow. The males of *Miniopterus* had small testes, while the embryos in the females had made a large advance in size. A single nest of *Pachycephala* containing eggs was found, evidently produced by a straggler from the previous season. *Emoia* continued to breed, and indeed did so throughout the year, though not always at the same rate.

* *Garuga* was not observed during this month.

November.

This month was marked, as usual, by the beginning of wetter weather, though it must be remembered that there is no dry season in this part of the world. The sun passed overhead on its way south on the 14th; the temperatures shown by all the thermometers rose. The observed plants (except *Garuga*) remained in flower or fruit. No more pregnancy was found in *Pteropus*; the testes were continuing to grow in readiness for the next season. The embryos of *Miniopterus* had once more grown greatly. The testes of *Pachycephala* at last began to decrease in size, and nearly every adult of both sexes was moulting, at least in patches.

December.

Rainfall increased to a daily average of 18·3 mm., the highest for any month of the year. The temperature remained high. The longest day of the year, on the 21st, extended to 13 hours 2 minutes. Most of the observed plants remained in flower or fruit. The testes of *Pteropus* continued to grow. The embryos of *Miniopterus* increased to their maximum size and were born during this month (or perhaps early the next). The epididymides of the males were now empty of spermatozoa. *Pachycephala* was in full moult; the testes of the males dropped to their minimum weight, less than one-fortieth of what they were to reach at their maximum in July, and the majority contained no spermatozoa.

January.

The early part of the notopheuge or southern summer was hot and wet. The mean temperature for the month in the Stevenson screen reached its highest figure for the year (26·6° C.,=80° F.), but it is to be recollected that this was only 2·1° C. more than the mean temperature of the coolest month. All the observed plants, except *Garuga*, remained in flower or fruit. The testes of *Pteropus* reached their maximum size. The females of *Miniopterus* had now given birth to their young. The testes of *Pachycephala* were just beginning to increase in size.

February.

The weather remained hot and wet. The sun passed overhead on its way north on the 8th. Our botanical observations were unfortunately incomplete during this month, but the species on which we recorded observations were mostly still in flower or fruit. The only striking change among the observed animals was that some of the female *Pteropus* began to become pregnant.

March.

The weather was still hot and wet. The monthly mean of barometric pressure reached its lowest point this month, but this was only 0·23 inch less than its maximum in September. The general flowering season was now at an end: no flowers nor fruit were seen on *Corymborchis*, *Castanospermum*, *Eugenia*, *Barringtonia* or *Psychotria*, though *Ficus* still carried its figs and fruit was seen on *Piper*. There was no striking change among the observed animals. Some more *Pteropus* became pregnant and the testes of *Pachycephala* continued to increase steadily in size. The lizard, *Emoia*, at last began to breed less rapidly.

April.

The early part of the boredune or southern autumn brought a distinct change in the weather: there was a sharp decrease in rainfall and a noticeable increase in saturation deficiency. The mean daily period of sunshine reached its maximum for the year (6·9 hours), and the temperature remained high. In the forest the maximum and earth thermometers showed their highest monthly mean temperatures of the year. The average cooling power of the atmosphere in the forest, as shown by the dry katathermometer, reached its lowest figure for the year (3·5 millicalories per

square centimetre per second). Nearly all the observed plants, including *Ficus* and *Piper*, were now without flowers or fruit. The main pregnancy-season of *Pteropus* began (though occasional females had been pregnant in the two previous months). The testes of *Pachycephala* continued to increase steadily in size as the days grew shorter.

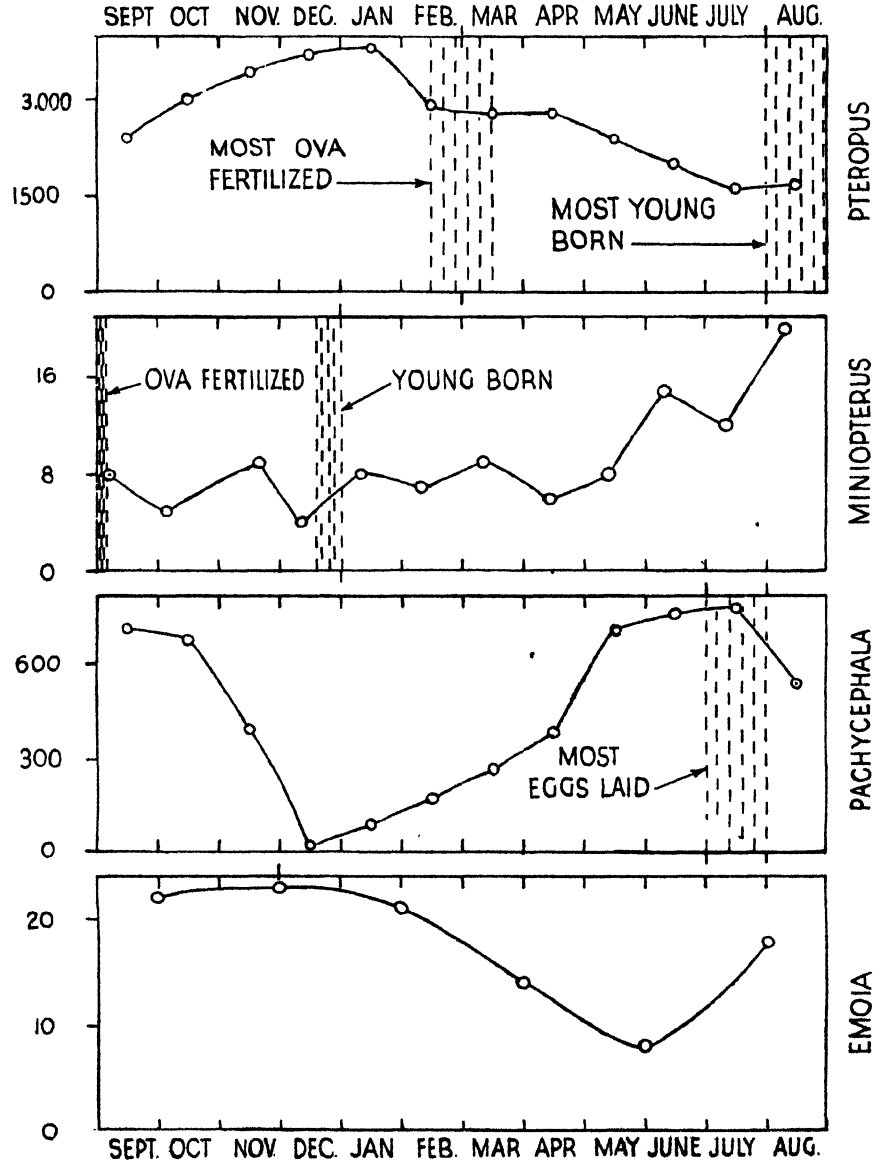

FIG. 1.—Graphs showing the mean weights of the testes of adult males of the observed animals throughout the year (1933–4). The ordinates represent the weights of both testes in milligrams. The seasons when ova were fertilized, etc., are also indicated.

MAY.

The weather remained relatively dry and hot. This month and the last were the only ones in which the saturation deficiency of the atmosphere in the forest was noticeably above the average for the year. The mean temperature in the forest now reached its maximum for the year, considerably later than it was reached in the Stevenson screen in the open. Several of the observed plants, which had been in a non-reproductive phase in March or April, were now in flower or fruit again (*Piper, Eugenia, Barringtonia*, and *Psychotria*). Most of the embryos of *Pteropus* were considerably larger than in the previous month. The testes of *Pachycephala* continued to increase in size, and an egg was found in an oviduct of a single female. The lizard, *Emoia*, now reached a low point in its breeding cycle : only two ovigerous females were observed during the month, and the mean weight of the testes of adults had sunk to about one-third of the maximum reached in November and December.

JUNE.

June was relatively dry and somewhat cooler. The shortest day of the year, on the 21st, extended to 11 hours 14 minutes. *Corymborchis* and *Ficus* started to reproduce again. This and the preceding month witnessed a subsidiary flowering season in a number of plants in which the main season was about September to about January or February. Most of the embryos of *Pteropus* were now larger again, though some very small ones showed that eggs were still being fertilized ; but the mean weight of the testes had greatly decreased from its maximum in January. The testes of *Miniopterus* now at last started to grow. Those of *Pachycephala* had nearly reached their maximum. Young were found in a nest, but the main breeding season had not yet started. Only a single ovigerous *Emoia* was found during the month, and the testes of this species remained small.

JULY.

The early part of the borepheuge or southern winter was relatively dry and cool. All the thermometers registered their lowest means of the year either this month or the next. The cooling power of the atmosphere in the forest, as shown by the dry katathermometer, reached its highest monthly mean of the year (5·27 millicalories per square centimetre per second). The mean daily hours of sunshine reached their minimum for the year (3·5 hours). Several of the observed plants were no longer reproducing, their subsidiary flowering season being at an end. Most of the embryos of *Pteropus* were now large. A few very small embryos showed that fertilization was still occurring sporadically although the testes had reached their minimum size for the year. Most of the adult male *Miniopterus* now had their epididymides once more crowded with spermatozoa. This month was the main egg-season of *Pachycephala*. The testes reached their maximum weight, more than forty times the December minimum. 18 nests containing living eggs or young were found, while only three such nests were found during the whole of the rest of the year. *Emoia* was starting to reproduce more rapidly in this and the succeeding month.

AUGUST.

The weather remained relatively dry and cool. The earth thermometer and the minimum thermometer in the forest, as well as the minimum thermometer in the Stevenson screen and the grass-minimum thermometer in the open all recorded the lowest means of the year. Two of the observed plants (*Barringtonia* and *Psychotria*) started reproduction again, while most of the others were still without flowers or fruit. The embryos of *Pteropus* reached their maximum size (two exceeded 80 grams each), and most of them were probably born this month. Fertilization had now ceased, for no more very early pregnancies were seen, though there were quite a number of medium-sized embryos which would probably not be born until October.

The testes of *Miniopterus* now reached their maximum size, presumably in readiness for fertilizing the females early next month as they did the year before. The epididymides were crowded with spermatozoa. The breeding of *Pachycephala* was now almost at an end: only a single new nest was found, which contained young birds, and the size of the testes was falling off.

The reader who has followed this summary of the seasonal changes will have noticed that although the mean temperature of the hottest and coolest months only differed by 2·1° C. and the longest day was only about 1¾ hour longer than the shortest, and although there was a daily average of 3·9 mm. of rain even in the least wet month, yet most of the terrestrial organisms showed marked seasonal changes in their reproductive behaviour. Most of the observed plants had a long and a short reproductive season during the year, though the herb *Geophila* reproduced continuously and *Ficus* and *Piper* nearly continuously, like *Lamium purpureum* in Britain. Of the vertebrates observed, only the lizard, *Emoia cyanura*, reproduced continuously, and even here there was almost a cessation during two months. (*Emoia werneri* probably stopped reproduction altogether during one month in 1927.) The male *Pteropus* retained spermatozoa in the epididymides throughout the year, but the testes underwent a regular cyclical change in weight, and there was a distinct breeding season, the females mostly becoming pregnant about March. *Miniopterus* showed the sharpest possible breeding season. The evidence shows that all the females that bore young became pregnant about the first few days of September: the fertilization of ova was entirely confined to these few days of the year. (The fourth paper in this series should be consulted for the evidence on which this statement is based.) Afterwards the epididymides of the males lost all their spermatozoa. No animal living in a strongly seasonal climate could have a more sharply defined breeding season. This seems all the more extraordinary when it is remembered that this little bat hangs throughout the period of daylight, till about ten minutes before sunset, in a dark and almost thermostatic cave. *Pachycephala*, again, has as sharp a breeding season as most British birds, with the greater part of the egg-laying crowded into a period of about a month. At one time of year the testes are more than forty times as heavy as they are at another, and when they are at their minimum they contain no spermatozoa.

Briefly, then, the mammals and bird studied are at least as seasonal in their reproductive behaviour as the mammals and birds of temperate climates. However, the various animals reproduce at times of year that bear no obvious relation to the breeding seasons of temperate lands. Thus the passerine bird breeds very early in the southern 'winter', while the insectivorous bat copulates not in the 'autumn', but at the end of the southern 'winter', and the development of the embryos proceeds at once without any latent period.

Although the other fruit-bat, *Pteropus cotinus*, was not studied nearly so intensively as *Pt. geddiei*, sufficient data were obtained to show that its breeding season is approximately the same.

Are the breeding seasons annually recurrent?

Since the Oxford University Expedition only lasted for 366 days, it could not collect definite evidence to show whether the breeding seasons of the animals studied recur annually at about the same time, or whether, on the contrary, they recur irregularly in different years, or regularly at periods exceeding twelve months. This is a matter requiring careful consideration.

It is relevant to note first the evidence presented by the phenomena of periodicity in the plants. It has been mentioned that the deciduous tree, *Garuga*, was without leaves at the beginning of September but regained them during that month. The Rev. W. Anderson, who lives at Hog Harbour, kindly agreed to make observations over a period of years. He made reports in 1936, 1937, 1938, 1941 and 1942, as well

as a general statement in 1944. *Garuga* is clearly deciduous at about the same season annually. It usually begins to lose its leaves about the end of June and becomes leafless in July. The leaves appear again in September. In 1942 the leaves were lost about a month earlier than usual. Mr. Anderson attributed this to the very dry weather.

Garuga, then, has an annual season of leaf-fall. No data over a period of years are available for other plants, but the forest-trees *Erythrina indica* (Papilionaceae) and *Alphitonia zizyphoides* (Rhamnaceae) are evidently regularly periodical, for the natives rely upon their flowering to fix the time for the annual planting of yams and sweet potatoes respectively.

The evidence that the reproductive periodicity of the animals is annual rests mostly on indirect evidence, but the following ten arguments suggests strongly that it is :—

(1) The writer studied the weight of the testes of *Pteropus* at Hog Harbour from January to July 1927, and there was a very close resemblance between the change of weight during these months in 1927 and 1934. (See p. 132 of the third paper in this series.)

(2) In 1927 the writer found that the embryos of *Pteropus* grew steadily from February till July and were born late in that month or in August. This closely corresponds with what happened in 1934.

(3) *Pteropus* was at the tail-end of its pregnancy-season in September and October 1933 ; the following August the cycle had come round again and young were being produced, while medium-sized embryos in some of the females showed that the pregnancy-season would again straggle on till October.

(4) The graph showing the weight of the testes of *Pteropus* throughout the year would join on smoothly to another similar graph placed beyond it.

(5) In *Miniopterus* fertilization occurred during the first few days of September 1933 and at no other time during the year ; in correspondence with this, the testes attained their maximum size in August of the following year.

(6) A single nest of *Pachycephala*, containing eggs, was found early in October 1933, but no nest thereafter till June 1934 ; this agrees well with the fact that the main egg-season occurred in July, 1934. The October nest was presumably produced by a straggler breeding later than most of the species.

(7) The testes of *Pachycephala* were large in September 1933 and again in August 1934.

(8) By a study of skins of *Pachycephala* taken in the northern New Hebrides in 1926–7, Mayr (1932) found that January was the season of full moult. This agrees sufficiently well with the full moult season in 1933–4 (December : observations on moulting were not made in January).

(9) The graph showing the weights of the testes of *Emoia cyanura* throughout the year would join on smoothly to another similar graph placed beyond it.

(10) The writer studied the reproduction of the closely related *Emoia werneri* at Hog Harbour throughout 1927. The breeding cycle was closely similar to that of *E. cyanura* in 1933–4, the only difference being that whereas *E. cyanura* nearly stopped breeding in May, *E. werneri* appears to have done so altogether in the same month. In both cases reproduction was at its height in November and December. (See the sixth paper in this series.)

These arguments, taken together, almost prove that the breeding cycles are annually recurrent. It is the writer's hope that he or some one else will have an opportunity to obtain conclusive evidence on this matter. To do this it would not be necessary to spend a whole year at Hog Harbour : it would suffice to remain from June or July till September or October. If *Pteropus* showed large embryos in July

and August, if *Miniopterus* females became pregnant in August or September, if *Pachycephala* showed an egg-season about July, and if *Emoia* increased its reproductive activity during the period of study, the proof would be conclusive.

The causes of the breeding seasons.

The causes of breeding seasons may be analysed thus (Baker, 1938):

Ultimate causes

Proximate causes { internal rhythm / external (environmental) factors* }

The ultimate causes of breeding seasons are the reasons why it is beneficial for a species to breed only at a certain time of year. In temperate climates the young are usually hatched or born at a time of year that is obviously suited to their welfare. It is not possible to suggest what may be the ultimate causes of breeding seasons in the northern New Hebrides, for one cannot see why one season of the year should be preferable to another for the production of offspring. The young fruit-bats are born about August and the insectivorous bats in December, while the young *Pachycephala* hatch in July, and reproduction in the lizard, *Emoia*, reaches its maximum in November and December. One can only suggest that if reproduction continued throughout the year, the whole species might die out from the consequent elimination of the food-supply.

The proximate causes of breeding seasons are the influences that act upon individual animals and make them start and stop breeding at certain times of year. Although internal rhythm is an important auxiliary proximate cause of breeding seasons in some organisms, yet it can never act altogether independently of environmental control. This was proved conclusively, by *reductio ad absurdum*, on pp. 517–8 of the second paper in this series. It is necessary to consider what are the external (environmental) changes to which the vertebrates of the northern New Hebrides respond by starting or stopping breeding (or, in the case of *Emoia*, by breeding more rapidly or more slowly).

If a graph showing the reproductive activity of *Emoia* throughout the year is placed beside another showing the duration of daylight, as was done in the sixth paper in this series, the resemblance is obvious; for reproduction reaches its maximum in the long days of November-December and its minimum in the short ones of May–June. It must not be taken for granted, however, that this is a case of cause and effect, for *Pachycephala* behaves in the opposite way. From their minimum size in December the testes grow larger by regular monthly increments during the whole of the period (January to June) while the days are growing shorter; and while the days are growing longer from October to December, the testes are becoming reduced to less than one-fortieth of their maximum size. Thus it is certain that increase in length of day is not the environmental factor that stimulates the growth of the testes in *Pachycephala*; and the start of the egg-season coincides almost exactly with the period of shortest days, at the time of year when the daily hours of sunshine are also at their minimum for the year. In *Pteropus*, again, the time when most of the females become pregnant is February and March, that is to say, part of the period during which the days are getting shorter. Duration of daylight obviously cannot influence the reproduction of *Miniopterus*, which only emerges from its dark cave at nightfall.

Although the daily duration of illumination can profoundly influence the reproduction of birds (Rowan, 1926) and mammals (Baker and Ranson, 1932; Bissonnette, 1932), yet there is a tendency to exaggerate the part it plays in the control of breeding seasons.

* External factors are sometimes called 'exteroceptive' factors, but this is undesirable. 'Exteroceptive' means 'receptive of external stimuli' and is applicable only to the organism, not to the environment.

In most tropical countries there is a distinct dry season, and there is strong evidence that the start of the rainy season is a stimulant to the reproduction of many birds; but in the northern New Hebrides there is no dry season, and the breeding season of *Pachycephala* falls in the less wet season of the year. The saturation deficiency of the atmosphere in the forest was markedly less in April and May than in the other months of the year, but this cannot be correlated with changes in the reproductive cycles of any of the animals studied.

Pachycephala bred during the cooler part of the year, and the very short copulating season of *Miniopterus* fell also during this period. *Pteropus* copulated during the hotter part of the year, during which also the reproduction of *Emoia* reached its maximum. The difference in mean temperature between the hottest and coolest month was so small (2·1° C.) that it is not very easy to believe that it could be the controlling factor. It is worth remembering, however, that the dry katathermometer showed considerable changes in the cooling power of the atmosphere in the forest during the year. This varied from a mean of only 3·5 millicalories per square centimetre per second in April to a mean of 5·27 millicalories in July, during the period of the trade winds.

Pteropus is frugivorous and *Miniopterus*, *Pachycephala* and *Lygosoma* insectivorous. The expedition was not able to discover any change in food-supply that would be likely to affect reproduction. Some of the fruits eaten by *Pteropus* are only available during a part of the year.

The barometric pressure varied remarkably regularly during the year, but the difference between the mean figures for the months of highest and lowest pressure was only 0·23 inch, and this is scarcely likely to influence reproduction.

The facts suggest strongly that the breeding seasons of the vertebrates of the northern New Hebrides are controlled by environmental factors of a totally unsuspected kind, not affecting the sense-organs or meteorological instruments of man. This conclusion is forced upon one above all by the astonishing behaviour of the insectivorous bat, *Miniopterus*, which hung all day in a dark and almost thermostatic cave situated in one of the most unvarying climates in the world, yet never fertilized its eggs throughout the year of observation except during a few days at the beginning of September, when most of the adult females suddenly become pregnant.

Acknowledgements.—The expedition to the New Hebrides in 1933–4 was made under the auspices of the Oxford University Exploration Club. Contributions to the funds of the expedition were made by the Royal Society, the Percy Sladen Memorial Fund, the University of Oxford, and New College, Oxford. Before the expedition left England valuable advice on meteorology was given by Prof. P. A. Buxton and Mr. W. G. Kendrew. In the islands help was given especially by the British and French Resident Commissioners, the Rev. W. Anderson, Mrs. Anderson and Mr. T. R. ff. Salisbury, as well as by many native friends, who were keen natural historians. The expedition's vertebrates were identified by Mr. A. Fellows, Mr. N. B. Kinnear and Mr. H. W. Parker. The Keeper of the Department of Botany at the British Museum (Natural History) took charge of the expedition's plants, which were identified by Mr. J. E. Dandy, Mr. A. W. Exell, Mr. J. S. L. Gilmour, Prof. A. Guillaumin, and Dr. G. Taylor. Prof. Guillaumin (1938) has published a flora of the island of Espiritu Santo, based on the expedition's collections. The results of the expedition's work on breeding seasons were worked out in the Department of Zoology and Comparative Anatomy at Oxford, by permission of Prof. E. S. Goodrich and with the benefit of his advice. On behalf of the expedition the writer offers his thanks to the above-mentioned persons and institutions for all their help. He expresses particular gratitude to the Rev. W. Anderson and Mrs. Anderson for their kindness and helpfulness during his visits to the New Hebrides in 1922–3, 1927 and 1933–4, and to the Percy Sladen Trustees for supporting all three expeditions.

Summary.—The following is an attempt to summarize this paper, which is itself a summary :—

(1) The vicinity of Hog Harbour, 15° S. in the New Hebrides, Pacific Ocean, was chosen for a study of the breeding seasons of vertebrates in a particularly unvarying tropical rain-forest region. The mean temperature of the hottest month is only about 2° C. higher than that of the coolest, and there is no dry season (though one part of the year is wetter than the other).

(2) The animals chosen for intensive study were a fruit-bat (*Pteropus geddiei*), an insectivorous bat (*Miniopterus australis*), a passerine bird (*Pachycephala pectoralis*) and a lizard (the skink, *Emoia cyanura*).

(3) *Pteropus*, *Miniopterus* and *Pachycephala* each had one breeding season during the year of observation. The main period of fertilization of ova was February and March for *Pteropus*, early September for *Miniopterus*, and July for *Pachycephala*. *Emoia* bred throughout the year, but much more rapidly during November and December than during May and June.

(4) It is almost certain that the breeding seasons are annually recurrent.

(5) It is certain that increasing length of day does not stimulate the growth of the testes of *Pachycephala*. From their minimum size in December the testes grew larger by regular monthly increments throughout the period (January to June) during which the days were growing shorter ; and while the days were growing longer from October to December, the testes were shrinking to less than one-fortieth of their maximum size.

(6) *Miniopterus* hangs throughout the period of daylight till about ten minutes before sunset in a dark and almost thermostatic cave situated in one of the most unvarying climates in the world, but it did not fertilize its eggs throughout the year of observation except during a few days about the beginning of September, when most of the adult females suddenly became pregnant.

(7) It seems probable that the breeding seasons of the animals investigated are regulated by some altogether unsuspected cause or causes.

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The six previous papers in this series on ' The seasons in a tropical rain-forest (New Hebrides) ' are here listed separately for convenience of reference :—

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Contributions to the study of some African Mammals.—III. Adaptations in the bones of the fore-limb of the Lion, Leopard, and Cheetah.

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(With 5 Text-figures)

[Read 7 June 1945]

After spending some time on the study of the limb-bones of highly specialized cursorial animals such as the antelopes (Hopwood, 1936), it seemed desirable to extend one's observations to a more generalized kind. For this purpose the fore-limbs of the three big cats of the African fauna were selected because they offer the greatest variety within a single family. Generally speaking, the Lion lives either in sandy or semi-desert places where there is plenty of scrub in which to hide, or else in rank vegetation bordering water. It is not given to climbing trees, although it may scramble up a sloping trunk, and is never found far inside forests. Over short distances it can move as fast as a horse in a shuffling, shambling gallop, but its usual gait is a somewhat deliberate walk. The Leopard, on the other hand, lives in wooded country and climbs trees with ease. In areas where forests are absent, it lives in broken, rocky, scrub-covered places. As a rule it does not travel so far from its lair as does the Lion, neither is its greatest speed equal to that of the Lion. The Cheetah is never met with away from the open plains ; it obtains its prey by running it down, and over short distances of a few hundred yards is the swiftest of all mammals. These differences in habit should be reflected in the skeleton of the limbs, especially in that of the fore-limb which is much more characteristic than that of the hind-limb.

All the skeletons were obtained in the neighbourhood of Olduvai, on the eastern edge of the Serengeti plains, and are preserved in the Department of Zoology of the British Museum. Most of them were collected by Capt. J. R. H. Hewlett during Dr. Leakey's expedition of 1931.

Scapula. The scapulae of the Leopard and Cheetah are of about the same size, but that of the Cheetah is narrower, has a wider and shallower suprascapular notch, and a straighter anterior border. The spine overhangs the infraspinous fossa to a greater extent carrying the insertions of the trapezius and the origin of the deltoid farther back, and closer to the trunk, than they are in the Leopard. On the inner, or medial, surface of the bone the scar for the serratus magnus and levator anguli scapulae is placed almost entirely behind the spine ; it forms a rectangle which is deeper dorso-ventrally than it is wide. In the Leopard, on the other hand, this scar extends right across the position of the spine, and forms a diamond-shaped figure which is much wider antero-posteriorly than it is deep dorso-ventrally. Finally, the upper end of the axillary border has a pronounced inward curvature in the Cheetah, whereas in the Leopard the curvature is slight ; consequently, the insertions of the serratus magnus and rhomboideus major are nearer to the sagittal plane of the body of the Cheetah than they are to that of the Leopard.

As a whole, the scapula of the Lion resembles that of the Leopard rather than that of the Cheetah, but it agrees with that of the latter in having a rather straighter anterior border and a shallower, wider, suprascapular notch. The insertion of the spine to the body of the scapula is more oblique than it is in the Leopard, but not so oblique as in the Cheetah. On the inner surface the general shape and position of the insertions of the serratus magnus and levator anguli scapulae are much the same as those of the Leopard, but in the increased dorso-ventral depth an approach is made

to a Cheetah-like condition. The broad and massive metacromian processes of the Lion and Cheetah are in marked contrast to the Leopard's relatively slender hook; the origins of the levator claviculae and part of the spinous head of the deltoid are attached to this process. The acromion process is much stouter in the Lion than it is in either of the other species, from it the acromial portion of the deltoid takes its origin.

Of these three bones, that of the Leopard is the most generalized. The greater width, the more erect spine, the more diffuse and less concentrated muscle attachments, all of these facilitate a greater mobility of the shoulder. In the Lion, the rather more oblique spine limits the action of the trapezius and forces it to work more in one plane; at the same time, by taking the origin of the deltoid closer to the body, it limits the abductor function of the muscle. The serratus magnus and levator anguli scapulae are responsible for the backwards and forwards motion of the scapula and their efficiency increases with the dorso-ventral depth of their insertions. They also raise the thorax, and the efficiency of this movement depends on the antero-posterior width of the insertion. Evidently, therefore, movement to and fro is more important

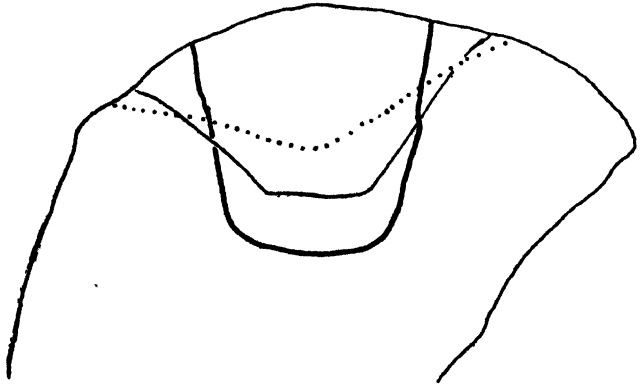


FIG. 1.—Diagram of the upper part of the medial surface of the scapula to show the differing shape of the area of insertion of the mm. serratus magnus et levator anguli scapulae in the Leopard (dotted), Lion (continuous), and Cheetah (heavy). Not to scale.

to the Cheetah, because it directly affects the speed of the animal, whereas in the Leopard most stress is laid upon raising the thorax, which is important in climbing. The scapula of the Lion is intermediate in type; the speed of its gallop is reflected in the shape of the muscle scars, and the need for a relatively mobile shoulder is to be seen in those points in which it resembles the Leopard rather than the Cheetah.

Humerus. The humeri of the Lion and the Cheetah differ from that of the Leopard in contrasting ways; that of the Lion, as befits so large and powerful an animal, is more massive, whereas that of the Cheetah is laterally compressed and more slender. In consequence of the lateral compression, the greater tuberosity of the Cheetah is more nearly parallel to the sagittal plane of the humerus than it is in either of the other two species; it is also taller, and the insertion of the infraspinatus is above the level of the head of the humerus, whereas, in the Lion and the Leopard this insertion is at the same level as the head.

Viewed from above, the insertions of the supraspinatus to the greater, and of the subscapularis to the lesser tuberosity are visible. Because of the lateral compression, the insertion of the supraspinatus forms a smaller angle to the sagittal plane of the head in the Cheetah than it does in the other two species; 15° to 20° as compared

with 30° in the Lion and Leopard. But if the Lion agrees with the Leopard in this respect, it approaches the Cheetah rather than the Leopard in the manner of the insertion of the subscapularis. In all three species this insertion passes backwards and downwards, but, whereas in the Leopard only the anterior one-third of the insertion faces upwards and the remainder inwards towards the trunk, half the scar faces upwards in the Lion and the remainder is not so markedly inward facing. In the Cheetah the scar faces inwards hardly at all, and the chief feature on the medial aspect is the sharp angle which forms the proximal margin of the tuberosity.

The chief features on the shaft are the humeral crest and deltoid tuberosity, the linea tuberculi majoris, and the teres tubercle ; all of these vary in position according to the species. The insertion of the teres minor is about equidistant between the anterior and posterior margins of the bone in the Cheetah ; even in the adult male the deltoid tuberosity is very small and indistinct whereas the backwards-facing tubercle for the insertion of the teres minor is prominent. In the Leopard the insertion of the teres minor forms a relatively large, pyramidal tubercle, which is much more distinct than the insertion of the deltoid and is nearer the posterior than it is to the anterior margin of the bone. The deltoid tuberosity is approximately equidistant between the anterior and posterior margins of the lateral surface of the shaft, on which it forms a sharp ridge. Conditions in the Lion are to some extent intermediate between those in the other two species. The insertion of the teres minor is distinct but generalized ; the deltoid tuberosity is less than one-third of the width of the shaft from the anterior margin, and is stronger than it is in either of the other species. The insertion of the teres minor is intermediate in position between that of the Leopard and the Cheetah. The most important feature on the medial aspect of the shaft is the teres tubercle. Its variation may be most easily estimated by imagining a line drawn across the shaft so as to mark off the proximal third. If this be done, then the lower end of the teres tubercle of the Leopard touches the line, that of the Lion is below the line, and that of the Cheetah is well above it. Sometimes the teres tubercle of the Leopard approximates in position to that of the Lion, though it is never quite so low, but it appears to be an invariable rule that in all three species the centre of the tubercle is directly opposite to that of the deltoid tuberosity. Both the Lion and the Leopard have the humeral crest and the linea tuberculi majoris widely separated as far as the deltoid tuberosity, below which the humeral crest turns more or less sharply to meet the linea tuberculi majoris. The humeral crest of the Cheetah does not change its direction at the deltoid tuberosity, but continues in an even sweep throughout its course.

The medial epicondyle, to which the flexor muscles of the hand are attached, is large and salient in the Lion and Leopard, but forms a low dome in the Cheetah. Both the Lion and the Leopard display a linear arrangement of the muscle attachments to the epicondyle, but whereas in the Lion this line forms an angle of about 45° with the inferior margin of the trochlea, the corresponding angle in the Leopard is about 75° bringing the line of attachments more nearly parallel to the length of the shaft. In the Cheetah the scars have a crescentic arrangement, with the concavity facing upwards and backwards. The differences between the lateral epicondyles of the three species are slight and inconstant.

There do not appear to be any outstanding differences between the distal articular surfaces of the humeri of the Lion and Leopard, but the margins of the trochlea, both lateral and medial, are more nearly parallel to the sagittal plane of the shaft in the Cheetah than they are in the other two species.

The muscles of the shoulder and arm are best considered under the well-known heads of extensors and flexors ; some of them have other functions as well, but for our present purpose those functions are of secondary importance. The most important extensor is the supraspinatus which is reinforced by the sub-scapularis and, depending on the position of the head of the humerus in the glenoid cavity of the scapula, by

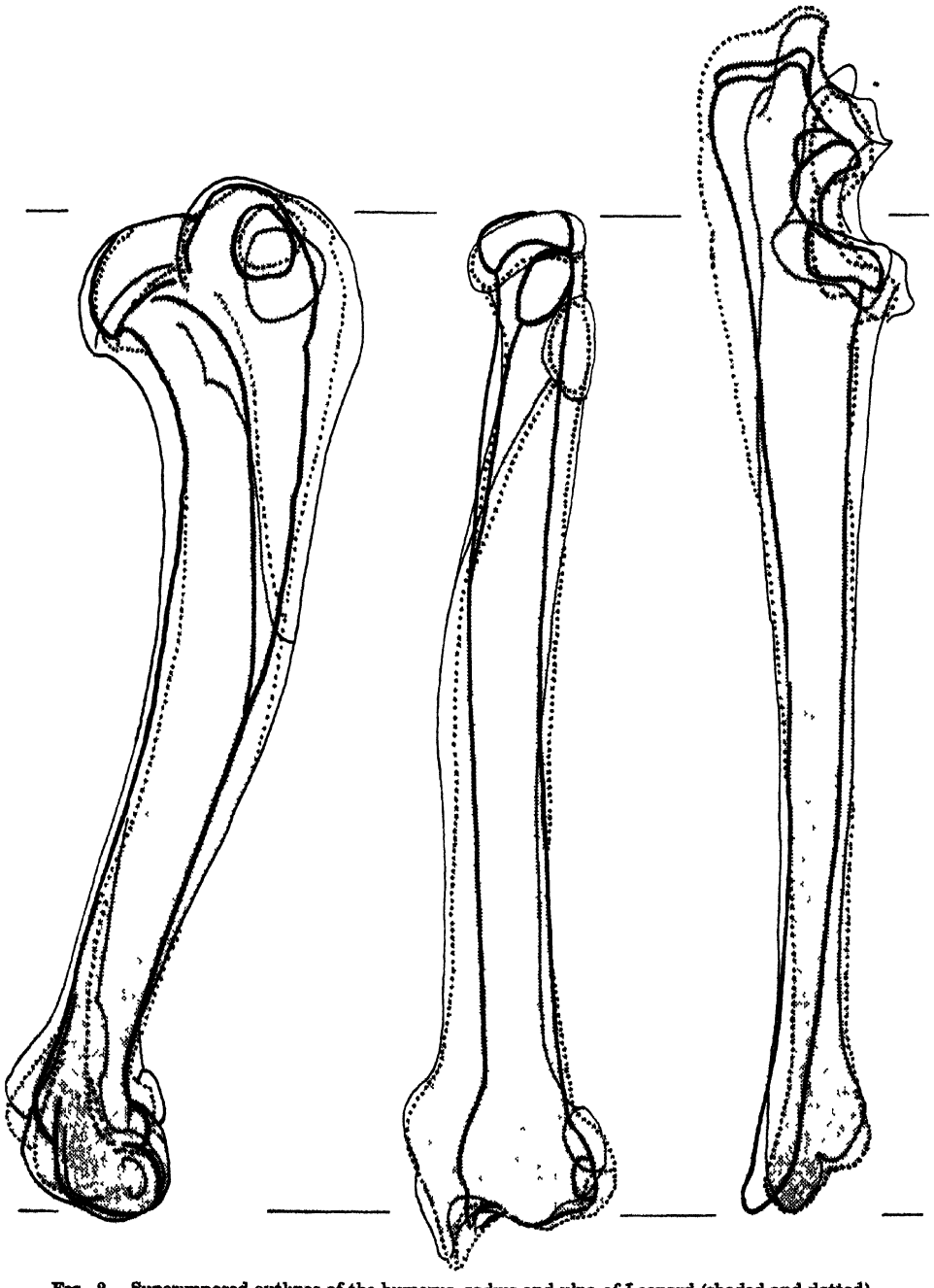


FIG. 2.—Superimposed outlines of the humerus, radius and ulna of Leopard (shaded and dotted), Lion (continuous), and Cheetah (heavy). The vertical distance between the horizontal lines is a common length to which all the outlines were reduced in order to make the relative proportions visible at a glance.

the infra-spinatus, both of them exercising secondary functions. The flexor group is made up of the deltoid, the latissimus dorsi, the teres major and the teres minor. According to the position of the head of the humerus, they may be reinforced by the infraspinatus.

This contrast in number and mass of the two groups of muscles is, of course, a reflection of the difference between advancing the fore-limb and restoring it to its normal position beneath the trunk. When moving, the animal first flexes the fore-limb to raise it from the ground and then extends it ; in so doing the energy used is that required to overcome the inertia of the limb. Once the limb touches the ground it is fixed and the body-weight has to be moved forward to it. This weight is moved partly by the push of the hind-limbs, and partly by the pull of the fore-limbs. The pull is largely provided by the latissimus dorsi and pectoralis profundus, which draw the body up to the limb, but it is supplemented by the action of the muscles which flex the shoulder as the body moves forward. This more or less passive drag exercised by the flexor group is in contrast to the active pull of the latissimus dorsi and pectoralis profundus, nevertheless, it is important because the total mass of the flexores is, to some extent, determined by the proportion of the inertia of the trunk which they overcome in flexing the limb.

From these general considerations we may pass on to consider in some detail the action of the more important muscles inserted to the humerus, and to notice how the manner of their insertion and the amount of the lateral compression of the humerus affect the movement of the bone. The relative amount of lateral compression may be estimated by comparing the medio-lateral diameter at the level of the deltoid tuberosity with the antero-posterior diameter at the same level. Approximate values are, Leopard 75%, Lion 70%, Cheetah 57%. The reduction of the transverse diameter of the humerus reduces the mechanical advantage of the abductor muscles, and limits the sideways motion of the limb.

Taken in the order in which they are mentioned in the description of the bones, the principal muscles inserted to the humerus, and their functions, are :

infraspinatus, inserts to the lateral surface of the greater tuberosity ; abducts and rotates the arm. According to the position of the caput humeri within the glenoid cavity of the scapula, the muscle may act as a flexor or as an extensor.

supraspinatus, inserts mainly to the medial surface of the greater tuberosity ; extends the shoulder joint.

subscapularis, inserts to the lesser tuberosity ; extends the shoulder joint, advances and adducts the arm.

deltoid, inserts to the deltoid tuberosity ; flexes the shoulder joint and abducts the arm.

teres minor, inserts to the proximal portion of the humeral crest between the insertion of the infraspinatus and the origin of the anconaeus externus ; flexes the shoulder joint and abducts the arm.

latissimus dorsi, inserted to the teres tubercle in common with the teres major ; flexes the shoulder joint and moves the humerus upwards and backwards. If the limb is fixed in an advanced position, it draws the trunk forward.

teres major, inserts to the teres tubercle in common with the latissimus dorsi ; flexes the shoulder joint, retracts and adducts the arm.

pectoralis profundus, inserts to the lesser tuberosity ; retracts and adducts the arm.

Since the insertion of the infraspinatus of the Cheetah is more nearly parallel to the sagittal plane than it is in either of the other species, the rotatory function of the muscle is lessened, and the position of the insertion relative to the caput humeri has the further effect of diminishing the abductor function. A similar limitation in the

movement of the limb of the Cheetah is indicated by the insertion of the supra-spinatus. Not only does its insertion to the greater tuberosity make a smaller angle to the sagittal plane of the head of the humerus than in either the Leopard or the Lion, but it is more concentrated towards the anterior margin of the tuberosity. Hence the extensor function of this muscle is emphasized in the Cheetah, and there is less possibility of a lateral excursus as the limb moves too and fro.

In the characters of the insertion of the subscapularis and pectoralis profundus muscles, the Lion is clearly intermediate between the Leopard and the Cheetah; it is evident that, whereas the former lays most stress on the adductor function as being of great importance to a climbing animal, and the latter on the extension of the shoulder and forward movement of the arm, to the Lion both functions are of equal value.

As a general rule, the greater the variety of movement of which a limb is capable, the less well defined are the insertions of muscles which perform more than one function. If, however, one function is exercised more than another, then the preponderance of that function is made evident in the character of the muscle scar. This is illustrated by the insertion of the teres minor, which forms a distinct tubercle in the Cheetah, but which is more or less diffuse in the Lion. Having regard to the double function of the muscle, and the mobility of the fore-limb of the Leopard, one might expect that the insertion would be diffuse in that species also, but the muscle is in fact inserted to a relatively large pyramidal tubercle. In the Cheetah the muscle scar is roughened and faces backwards, and its peculiar tubercle has evidently arisen from the need to provide a sufficiently large insertion for a powerful flexor muscle working entirely in one plane. In the Leopard the abductor function comes into play, causing the tubercle to be produced laterally and to form a definite pyramid. Neither flexion nor abduction has the pre-eminence in the Lion, consequently the insertion remains in the more primitive, diffuse state.

This study of the insertions of the teres minor is apt to be misleading for it implies that abduction of the fore-limb is more important to the Leopard than it is to the Lion. But when the insertion of the deltoid, which is primarily an abductor muscle, is considered, the position appears to be reversed, for the deltoid tuberosity of the Lion is stouter than that of the Leopard. In the sum, therefore, it is not the function itself, but the point at which the forces which exercise the function are applied to the humerus which is variable. That point is nearer the proximal end of the bone in the Leopard than it is in the Lion. The deltoid tuberosity of the Cheetah is not much more than a barely perceptible thickening of the deltoid ridge. By its lack of development, it confirms the relative unimportance of the abductor function of the muscle in this genus.

All three species have a teres tubercle of about the same relative strength. This is in accordance with expectation, because the functions of the latissimus dorsi and teres major are of absolute importance, irrespective of the type of adaption of the limb.

Radius. The radius of the Cheetah is slender, graceful, and relatively straight, whereas that of the Lion is stout, rugged, and strongly curved. The radius of the Leopard most nearly resembles that of the Lion in its general character and surface markings, but the curvature is less. The insertion of the long collateral ligament of the elbow is marked by a pronounced tubercle in the Lion and the Leopard but despite the greater size of the bone this tubercle is not so prominent in the Cheetah as in the Leopard. Old male Lions have the shorter ligament also inserted to a tubercle which is immediately below the head of the radius, but in the other two species, and in younger, though fully grown lions—as indicated by complete fusion of the epiphyses with the shaft, the place of insertion of this ligament is hardly to be discerned.

The prominent, ovate, tubercle for the insertion of the biceps is subject to a certain amount of individual variation but in the Cheetah it is nearer to the head of the

radius and more on the volar surface of the shaft than it is in either of the other species. The latter are also alike in the oblique line which arises from the lower third of the medial margin of the tubercle and passes downwards and inwards to the medial border of the bone, whereas in the Cheetah the same line takes its origin from the distal end of the medial margin of the tubercle and by following a less oblique course finally joins the medial margin of the bone well below the insertion of the pronator teres. In the Lion and Leopard the corresponding junction is effected at a point rather more than half-way between the head and the insertion of the pronator teres. The course of the oblique line is partly conditioned by the width of the bone, which is relatively greatest in the Lion and least in the Cheetah ; the greater the angle the oblique line makes with the long axis of the radius, the greater the breadth of the flexor profundus digitorum to which it gives origin, and the stronger that muscle is likely to be.

The lateral border of the radius is flattened in the Lion and the Leopard, whereas the medial border is relatively sharp ; consequently the cross-section of the shaft of the radius is more or less triangular, but in the Cheetah it is irregularly oval, the curvature being greater on the dorsal surface than it is on the volar. In the two former species the rough line for the interosseous ligament is on the volar edge of the flattened lateral border, but in the Cheetah it is entirely on the volar surface : there, at the centre of the shaft, it limits the lateral third of that surface, but it approaches the lateral margin of the bone at either end.

The position of the supinator brevis on the upper part of the dorsal surface of the shaft is marked by a very distinct flattening both in the Lion and in the Leopard, but in the Cheetah this same facet is scarcely to be detected. The differences in the insertion of the pronator teres are similar. In the Cheetah the insertion is not very distinct, whereas its position in the middle of the median border to one side of the distal end of the facet for the supinator brevis is clearly marked both in the Lion and in the Leopard.

The relative proportions of the distal end and of the styloid process are well shown in the figure. So far as the grooves for the extensor tendons are concerned, the Lion differs from the Leopard, and makes some approach to the Cheetah, in that those grooves in which lie the extensor carpi radialis and extensor carpi obliquus are somewhat narrower and deeper. In the Cheetah this process has been carried further and extended to the groove for the extensor communis digitorum. In none of the three is the groove for the extensor lateralis digitorum very distinct : it is best displayed in old male Lions. The facet which articulates with the distal end of the ulna is relatively large and distinct in the Lion and Leopard, but small and not well defined in the Cheetah.

The distal articular surface is concave in all directions, except where it passes on to the styloid process. There it tends to become convex in the volar dorsal direction, with the greatest convexity at the volar margin. This distal facet is broader and shallower in the Lion and Leopard, narrower and deeper in the Cheetah.

The foregoing account of the radius shows that the muscles of pronation and supination are more highly developed in the Leopard than they are in the Cheetah, and that the Lion is intermediate between the other two. Contrariwise, the extensor muscles of the Cheetah are relatively stronger than those of the Leopard, and again the Lion is intermediate. Once more the findings are what one might have anticipated from a general knowledge of the habits of the animals, for it is obvious that the power of rotating the forearm is of greater importance to a climbing species than it is to a cursorial one, and that powerful extensors are more likely to be found in the latter, where they are so valuable in maintaining the straightness and rigidity of the manus needed if the maximum speed is to be developed. The flexor muscles, on the other hand, are of greater importance to climbing animals, and we do in fact find that the origin of the deep digital flexor is clearly defined on the radius of the Leopard, and also

on that of the Lion, but that there is no particular feature to indicate its presence in the Cheetah.

Ulna. The proximal surface of the olecranon presents a domed fairly smooth, posterior area, and in front of it a deep fossa with prominent margins, one of them stronger and in advance of the other. The long head of the triceps is inserted to the posterior area ; the medial head to the medial margin of the fossa, and the anconaeus to the lateral margin.

There are significant differences in the development of the margins of the fossa. In the Leopard the lateral margin is thick and tumid ; it is pushed forwards in front of the medial margin, which is thin and sharp. In the Lion, too, the lateral margin of the fossa is the stronger and more forwardly situated of the two, but the medial

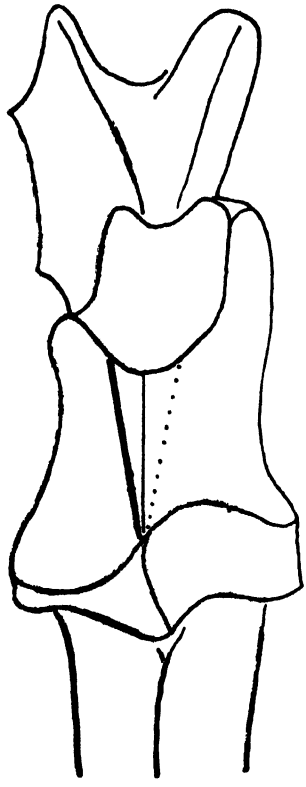


FIG. 3.—Diagram of the head of the ulna seen from in front, to show the position of the ridge in the sigmoid notch in the Leopard (dotted), Lion (continuous), and Cheetah (heavy). (The right side of the figure is the lateral side of the bone).

margin is relatively higher and stronger than it is in the Leopard. In the Cheetah the conditions are reversed and the medial margin is bigger, stronger, and more forwardly situated than the lateral. From these observations one may deduce that the Leopard has the anconaeus stronger than the medial head of the triceps ; that in the Lion the anconaeus is still the stronger, although the difference between the two muscles is less marked ; and that in the Cheetah the medial head of the triceps is much stronger than the head of the anconaeus.

The explanation of these variations in structure is evident when the greater sigmoid notch of the ulna is examined. This looks forwards and upwards, is concave from above downwards, and is divided by a low rounded ridge which extends from the anconeal process above to the lateral margin of the coronoid process below. If the plane of the ridge be continued upwards it cuts the proximal surface of the ulna in various ways, thus. In the Leopard it passes through the lateral lip, to which the anconaeus is inserted ; in the Lion it passes through the floor of the fossa, slightly nearer to the lateral than to the medial lip ; in the Cheetah it passes through the medial lip, to which the medial head of the triceps is inserted : this indicates a gradual migration of the longitudinal axis of the elbow-joint from without (Leopard) inwards (Cheetah), and a lessening of the angle between that axis and the long axis of the bone with the result that the forearm of the Cheetah moves more nearly in the same plane as the upper arm, whereas in the Leopard there is a marked difference between the two planes.

Both muscles are extensors of the elbow, and supplement the action of the long head of the triceps ; in addition they act as guides or distributors of the extending force and ensure that a proper proportion is applied to keeping the ridge of the sigmoid notch running truly within the groove of the trochlea of the humerus.

The shaft and distal end of the ulna are stout and well developed in the Lion and Leopard ; although the latter is perhaps the more slender, there are no great differences between them. Each has a prominent somewhat domed facet by which it articulates with the lower end of the radius and, separated from it by a deep notch, another facet of like character on the styloid process for articulation with the cuneiform and pisiform. In the Cheetah the shaft of the ulna is much more slender than in either of the other two species, and the distal end by no means so well developed. The facet for articulation with the distal end of the radius is greatly diminished and that for articulation with the cuneiform and pisiform, though distinct, is smaller still. The reduction of the shaft of the ulna and of its distal end in the Cheetah are bound up with a loss of the power of rotating the bones of the forearm, a function which ceases to be of use as the specialization for speed increases.

Carpus and Metacarpus. The carpus and metacarpus are most profitably to be considered as interarticulating units, and it is the nature of the articulations as entities rather than detailed descriptions of the individual bones which is significant. There are three joints involved, namely, the wrist, or radio-carpal, joint ; the inter-carpal joint ; and the carpo-metacarpal joint. Of these the shape of the first governs the movement of the wrist and hand relative to the forearm, the second gives added flexibility to the carpus and plays a major part in determining the degree of lateral motion of which the metacarpals are capable, and the third is largely concerned with the flexion and extension of the hand.

The radio-carpal joint is that between the distal end of the radius and the scapho-lunar bone. The radial facet of the latter is convex in both the medio-lateral and dorsi-volar directions and the former line is continued, laterally by the proximal ulnar, facet of the cuneiform. The dorsi-volar convexity is greatest on the lunar portion of the scapho-lunar and less on the scaphoid portion where it passes behind into a transverse concavity with a stout upward projection or lip. The lunar concavity in the Leopard is roughly hemispherical whereas the scaphoidal portion is somewhat flattened. In the Lion the lunar portion tends to be produced transversely to form a ridge. This is carried further in the Cheetah, so that a definite ridge extends right to the medial margin. The posterior lip of the concavity acts as a check ; it works into a small facet volar-lateral to, and just at the root of the styloid process of the radius, and limits flexion of the joint.

The transverse contour of the scapho-lunar is very nearly an arc of a circle, and the corresponding contour of the ulnar facet of the cuneiform is also an arc of a circle which is of greater radius than, and excentric to, the former. Consequently, lateral

motion of the wrist and hand on the forearm must entail a certain degree of separation between the distal ends of the radius and ulna, the separation being greatest in the Leopard, less in the Lion and least in the Cheetah. In none of the three species is there true articulation between the scapho-lunar and the cuneiform; the connexion is ligamentous. Extensive facets prove that the cuneiform and pisiform are in direct contact. The ulnar facet is largest and flattest in the Leopard, smallest in the Cheetah, and intermediate in extent but most deeply concave in the Lion.

The distal row of the carpus divides naturally into a radial portion (trapezium, trapezoid, magnum) and an ulnar portion (unciform), but the manner of its working is not so simple. The unciform has a lunar facet which is convex in front, and concave behind; the motion of the bone is dorsi-volar. The radial portion of the second row of the carpus divides into two parts, namely, the magnum, and the trapezoid

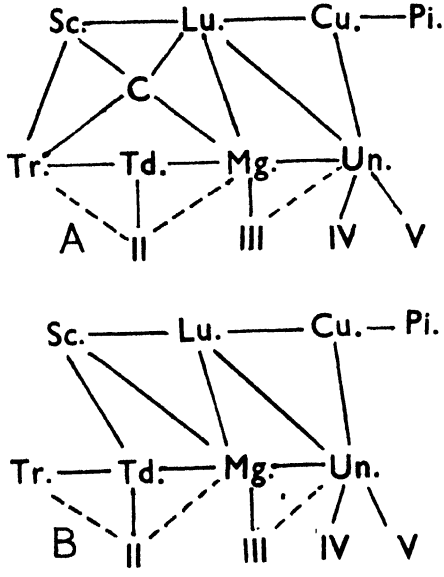


FIG. 4.—Carpal diagrams of a mesonychid creodont (A) and a hippopotamus (B). Full lines indicate primary, and broken lines secondary, contacts. Compare with fig. 5 on the facing page.

with the trapezium. The general direction of movement of the latter is conditioned by an oblique ridge which crosses the distal surface of the scapho-lunar from the antero-external to the postero-internal angle, and which engages with a groove on the proximal surface of the trapezoid. In the Lion and Leopard, but not in the Cheetah, this groove continues on to part of the proximal surface of the trapezium. Movement of the magnum is governed by an oblique groove which is to the ulnar side of the ridge just mentioned, and more directly dorsi-volar in direction; it engages with the proximal ridge of the magnum. In brief, there are three directions of movement of the distal row of carpal bones, all of them spreading fan-wise from the dorso-lateral angle of the scapho-lunar.

In the Lion and the Leopard the ridge for the trapezoid and the groove for the magnum cut the dorsal border of the inferior facet of the scapho-lunar at angles of about 38° and 67° respectively. In the Cheetah the groove for the magnum is strongly marked, but the ridge for the trapezoid is so greatly reduced that its value as a guide

is doubtful. Since the direction of the groove for the magnum has become more nearly dorsi-volar at the same time, and is now sub-parallel to the facet for the unciform, the effect is that the metacarpus and digits of the Cheetah are not so capable of being spread apart, and are forced to work more in one plane than they do in either of the other two species.

The carpo-metacarpal joint divides naturally into radial and ulnar portions. The radial portion consists of the first three carpals and metacarpals, and the ulnar portion of the unciform with the fourth and fifth metacarpals. Taken as a whole, the individual carpal bones are wedge-shaped, the dorsal surface being wider than the volar, so they form an arch of which the convexity is on the dorsal surface. The bases of the second and third metacarpals are also wedge-shaped (the much reduced first metacarpal may be ignored) and the grooves and ridges on their proximal surfaces diverge radially from a point behind the volar concavity to work against similarly divergent ridges and grooves on the distal facets of the second and third carpals.

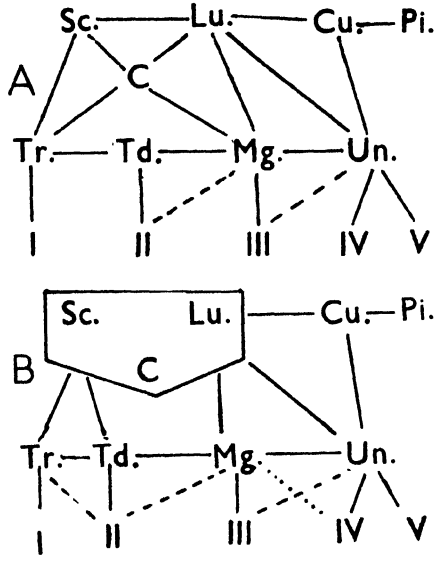


FIG. 5.—Carpal diagrams of a miacid creodont (A) and the three cats described in this paper (B). The contact between the magnum and the fourth metacarpal is indicated by the dotted line. Compare with fig. 4 on the facing page.

The bases of the fourth and fifth metacarpals are pressed closely together so their proximal articular surfaces form what is in effect a single segment of a transverse cylinder which articulates with the inferior facet of the unciform. A small facet on the postero-radial corner of the base of the fourth metacarpal articulates with the postero-ulnar corner of the magnum : it tends to be relatively larger in the Leopard than it is either in the Cheetah or in the Lion.

The distinctions between the carpo-metacarpal joints of Lion, Leopard, and Cheetah are, broadly speaking, of the same order as those already noted in other parts of the limb. In the Lion and Leopard the grooves and ridges on the radial portion are divergent and well-marked, whereas in the Cheetah they are sub-parallel, less distinct, and the whole surface of the distal carpals on which they occur is very much flatter in the Cheetah than in the other two species. The inter-metacarpal

articulations are best developed and most clearly defined in the Lion, and only less so in the Leopard. In the Cheetah they are reduced and by no means so clearly defined.

The differences noted between the articulations of wrist and hand of the Leopard and those of the Cheetah have the effect of restricting the range of movement of the latter. The radial-carpal articulation of the Leopard approximates to a universal joint, but the transverse extension of the convexity of the proximal facet of the scapho-lunar bone in the Cheetah limits the range of motion so severely that the universal joint of the Leopard, and to a lesser extent that of the Lion, is changed into a hinge which for all practical purposes moves only in an anterior-posterior direction. Similarly, the intercarpal joints of the Cheetah prevent that spreading of the metacarpus and digits which is so well developed in the Leopard and Lion. This restriction of movement is further reflected in the metacarpals of the Cheetah, the heads of which have the proximal facets much flattened. Moreover, the Cheetah has the metacarpals pressed closely together so that the third and fourth metacarpals incline to function as a unit, and the whole hand takes on a markedly artiodactyl character.

Discussion.—Owing to the form of the bones and the disposition of the muscles, the fore-limb of the Leopard is capable of a greater range and variety of movement than is that of the Cheetah ; the Lion comes somewhere in between the other two. The modifications of the Cheetah away from the general feline pattern are all in the direction of speed. They result in a diminution of the abductor function, in a pronounced tendency to restrict the limb to a backwards and forwards movement, in loss of the power of rotating the bones of the fore-limb, in a great reduction of the mobility of the carpus, and in pronounced artiodactyly of the metacarpus and digits.

The artiodactyly of the carnivore foot was first described by Boas, but his observations were confined to external characters. He also showed that artiodactyly, which is general and often well-marked among the Carnivora, occurs sporadically in other orders. There is, however, this difference, that whereas all genera of carnivores have paraxonic hands and feet, the other orders may also contain genera in which the symmetry is of the perissodactyl type (mesaxonic), and even genera in which the hand is of one type of symmetry and the foot of the other. Boas gives two examples among the rodents : *Hydrochoerus* has mesaxonic hands and feet, whereas the hares have a mesaxonic hand and a paraxonic foot.

Primitive artiodactyls preserve the original relationships of the distal carpalia to the metacarpalia almost unchanged. In them Mc I articulates with the trapezium, Mc II with the trapezoid, Mc III with the magnum, and Mc IV and V with the unciform. In some, at least, of the modern carnivora there is a small contact between the head of Mc IV and the volar-radial corner of the distal surface of the magnum, but this appears to be a feature which has developed *pari passu* with the gradual increase in size of the magnum. It is present on a few bones found in the Upper Eocene of France, and on bones found in later deposits, but it does not seem to be at all a constant feature until modern genera appear, and even in them there is reason to suppose that it is more regular in its development in the later species than it is in the earlier ones. Apart from this one character of doubtful value and meaning, the relations between the carpals and metacarpals are similar to those which obtain in that section of artiodactyls termed by Kowalevsky Artiodactyla Inadaptiva.

The differences which develop between the two orders when the carpal elements begin to fuse are also important. In the Carnivora the first step is for the centrale to unite with the scaphoid, and the next for the scapho-centrale to unite with the lunar to form the familiar scapho-lunar of the true carnivores. The Eocene Miacidae either have all the bones separate, or at the most a scapho-centrale, but one species, *Vulpavus profectus*, has a scapho-lunar of the modern type. The elements of the distal row never fuse in carnivores.

The artiodactyls, on the other hand, retain the discrete proximal row of carpal bones ; gradually lose the centrale, which never appears in recent genera, even as a cartilaginous vestige in the embryo ; and restrict fusion of the carpal elements to the radial side of the distal row. As a general rule, fusion takes place in the didactyl genera only, and the tetradactyl genera remain in the primitive condition, but there are exceptions. For example, the camel has all the bones of the carpus separate, and *Caenotherium*, an extinct tetradactyl genus, contains some species in which the trapezium, trapezoid, and magnum, are fused to form a single bone.

These observations indicate that although the Carnivora resemble the Artiodactyla in the symmetry of the metacarpus, they differ fundamentally in the characters of the carpus, and it might be thought that the resemblances were due to convergence. The true explanation is that the conditions governing the future evolution of the carnivore foot were laid down at the very beginning of the Tertiary, when the Miacidae, for reasons not yet fully understood, acquired a paraxonic symmetry. Once that had happened it was inevitable that further adaption towards a cursorial life should follow the same general lines as that of the artiodactyls, which also derive from a very primitive stock with paraxonic feet, the Mesonychidae. At the same time, it was not possible for the carnivores to follow exactly the same path as that trodden by the artiodactyls because the characters of the carpus differ, but it is worth remembering that the tendency so to do was very marked, and that the carnivores underwent a reduction of digits in the same manner, though not to the same degree, as the Artiodactyla Inadaptiva.

The Evolution of the Buffaloes, Oxen, Sheep and Goats.

By GUY E. PILGRIM, D.Sc., F.R.S. (Communicated by Dr. A. TINDELL HOPWOOD.)

(With 6 Text-figures and a diagram)

[Read 10 January 1946]

[This paper is the first half of a longer one left unfinished by Dr. Pilgrim when he died. The MS. of this part was in its final form, and the author had begun to type it. No draft of the second part, which was to have dealt with the relation of these groups to the remainder of the Pecora, was found.]

The Buffaloes, Oxen, Sheep and Goats, and the numerous types of Antelope form a single family, the Bovidae. They share with the Cervidae and the Giraffidae the possession of what we may collectively call 'horns'. This character, together with others, such as a hollow tympanic bulla, distinguishes these three families from the others of the large order Artiodactyla, of which they form the suborder Pecora (Latin,—*pecus*, *pecoris*, cattle).

The Pecoran 'horn' consists of three parts: (1) the outer skin, which in the Bovidae is changed into keratin; (2) the ossicone or *os cornu*, originally ossified from a centre separate from the skull and only united with it after birth; (3) a protuberance of the frontal bone of the skull. In the Giraffidae the ossicone constitutes by far the greater part of the 'horn', and its junction with the frontal is at first a simple suture such as we find between the other bones of the skull. In the two other Pecoran families, the frontal protuberance grows around and beyond the ossicone, and obliterates its individuality before the animal is born. In the Cervidae the 'horn', which is known as the antler, and is generally branched, is covered with a hairy skin in its young stages, but is bare when mature; it is shed and renewed annually. In the Bovidae both the horny sheath and bony core are permanent throughout the animal's life, except in the North American Prong-Bucks, sometimes put into a separate family as the Antilocapridae, which shed the horn-sheath periodically.

We infer from these details that the Giraffid horn is the most primitive, and that the other families have at some time in their history passed through a Giraffid stage. This is also suggested by the fact that horned animals showing Giraffid characters seem to appear earlier in the geological record than the Cervidae and Bovidae. In the lower Miocene primitive Giraffid genera, *Procervulus* and *Lagomeryx*, occur in Europe and China, and, probably, in America as *Dromomeryx*, *Aletomeryx*, and their numerous allies. Deer must have existed almost as early, if we may judge by the existence of an antlered type (*Stephanocemas*) in the lower Miocene of China and Europe.

The ancestors of these horned genera must have been hornless, and in many parts of the world we meet with such forms as early as the Oligocene; such are *Dremotherium* and *Amphitragulus* in Europe, *Blastomeryx* in America, and *Propalaeomeryx* in India. These clearly possess Pecoran characters and have been classed together under the general family name Palaeomerycidae. Some of them have been shown to possess all or nearly all the characters one would expect to find in the ancestors of the antlered deer of later periods, and certain hornless deer have survived to the present day, for example, the tiny Musk Deer (*Moschus*), and the Chinese Water Deer (*Hydropotes*). But we are not able to point with certainty to a form which stands

in similar relationship to the Giraffidae and the Bovidae, neither can we deny that any one of these hornless genera might be a common ancestor of all the Pecora. Horns were at first confined to the males, the females of the Bovidae and Giraffidae gradually acquired them later, and even now the process is incomplete. In the Cervidae the females have always remained hornless.

At a more remote period genera existed which show most of the characters to be expected in the primitive common ancestor of all the Pecora. These are *Gelocus* and *Prodremotherium* of the lower Oligocene of Europe, and *Archaeomeryx* of the upper Eocene of China. The two former genera belong to the family of the Chevrotains (Tragulidae), but they belong to a side branch which did not lead directly to the living species. The third genus may be more truly regarded as an ancestral Chevrotain, but, together with other genera which are less closely on the direct Pecoran ancestry, it has been classified as a distinct family, the Hypertragulidae.

The types chosen for the diagram (at the end of this paper) do not pretend to represent more than an approximation of the actual evolutionary stages and there are numerous gaps in the succession. As regards individual details of the anatomy, some of these gaps are partially filled by genera which, because of other features, are clearly off the direct line of ascent.

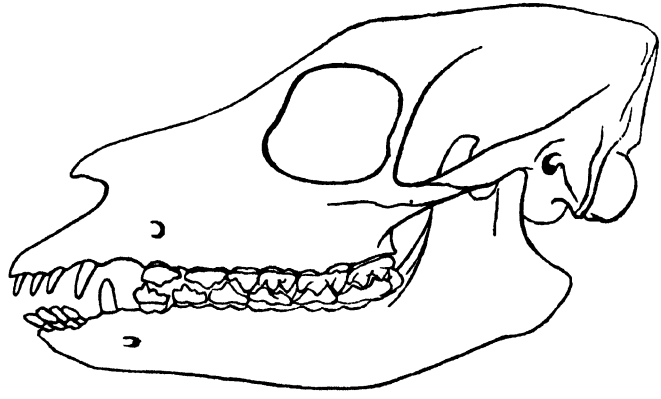


FIG. 1.—*Archaeomeryx optatus*. Restored skull and jaws, lateral view. Natural size. (Copied from Colbert, 1941, fig. 1A.)

ARCHAEOMERYX.—This was a small animal less than one foot high, which must have resembled the modern *Tragulus* in general appearance. It is known by a very complete series of fossils from the upper Eocene of China. It has been put into the family Hypertragulidae, of which the other members are American, but to all intents and purposes it is a primitive Tragulid, and there is good reason to believe that it is as near as may be to the primitive ancestor of all the Pecora.

The following are its most important primitive characters: skull hornless, face parallel to the basicranial axis, orbit in the centre line, brain-case small; upper incisors well developed, upper canine of medium size; of the three upper premolars retained, only the last approximates to the advanced Pecoran condition of crescents, the first two having simple cusps only; the upper molars are short-crowned, with rough enamel, and with four main cusps of which only the inner ones show any tendency to the crescent shape of the advanced Pecora; lower canine close to and shaped like the three incisors, all inclined strongly forward; front lower premolar with the shape and function of a canine, last three lower premolars composed of simple cusps without any trace of the complicated processes of the advanced Pecora, lower molars composed

of cusps of which only the outer ones show a tendency to the Pecoran crescentic shape ; in the front limb, the ulna strong and separate from the radius, median pair of digits separate, lateral digits complete but somewhat reduced so that the toes do not touch the ground ; the hind limb large, the navicular fused with the cuboid but separate from the ectocuneiform, median pair of digits separate, lateral digits complete, but more reduced than in the front foot.

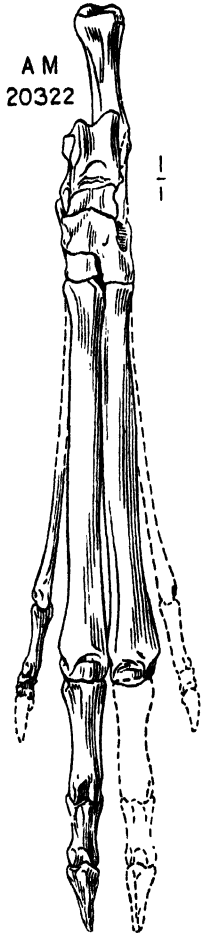


Fig. 2.—*Archaeomeryx optatus*. Left hind foot, dorsal view. Natural size. (Copied from Colbert, 1941, fig. 3.)

The following characters indicative of Pecoran relationships have been passed on to all the later members of the suborder ; orbit closed behind ; upper first premolar lost ; cusps in the upper molars reduced to four, most of the contemporary Artiodactyla have five or more ; the tendency to a crescentic shape in the inner cusps of the upper molars, and the outer cusps of the lower molars ; the complete loss of the first digit in both fore and hind feet ; fusion of the navicular and cuboid in

the ankle; reduction of the fibula to upper and lower vestiges, possibly unconnected in the middle even by a fibrous strand.

Gelocus.—This is an animal of more than twice the size of *Archaeomeryx*. Its remains have been found in the lower Oligocene of Europe, but are rather fragmentary. Of the skull only the upper and lower dentition are known. The upper incisors, as well as the first premolar, are possibly absent. The first lower premolar has been shifted back into the line of the others, and is a very small tooth; the upper molars are quite as short crowned as those of *Archaeomeryx*, but the internal cusps have assumed more of the Pecoran crescentic shape. The two median digits of the hind foot are now fused to form a cannon bone, but those of the fore foot still remain separate. In both feet the lateral digits are mere vestiges. The toes are not preserved. The fibula is known only by a vestige of its lower end.

Eotragus is the earliest undoubted Bovid with which we are at present acquainted. It has been found in the lower and middle Miocene deposits of Europe and Central Africa. The genus includes four species, all of them smaller than *Gelocus*, but of course a Gelocine smaller than those at present known may have existed, and have been the actual ancestor of *Eotragus*.

Eotragus retained many of the primitive characters of *Gelocus*, yet its possession of small, upright horns situated directly over the orbits, of upper and lower molars which have four distinct crescents, of upper premolars which have a single crescentic fold of enamel similar to those of the molars, and of lower premolars which have numerous complex folds, shows a very considerable advance on *Gelocus*. In fact, the progressive characters mentioned make it clear that *Eotragus* is a Bovid. The parallelism of the facial and basicranial axes, the presence of a large facial gland as shown by the pit for its reception, and the narrow triangular shape of the basi-occipital are primitive features which undergo considerable change in many of the later antelopes and especially in the Oxen and Sheep. *Eotragus* may have been the ancestor of the so-called Bovine Antelopes generally, but in any case it seems to lead directly to the subfamily Boselaphinae, which survives to-day in the Indian Nylghai (*Boselaphus*) and the Four-horned Antelope (*Tetracerus*), and through the subfamily to the Buffaloes and Oxen. The Sheep, however, must have branched off from an earlier Bovid, probably Gazelline, in the lower Miocene, since the twisted-horned genus *Oioceros*, whose geographical range extended from northern China to Europe, is closely allied to the Sheep and occurs first in the upper Miocene of China. The so-called Caprine Antelopes are no doubt descended from the same unknown lower Miocene Gazelle.

Pachyportax.—With this genus we reach a developmental stage which may be said to forecast the entrance of the Buffaloes and Oxen. It is known by two species, both of them Indian. The first, *P. nagrii* from the upper Miocene, is represented by a female skull without horns; it was about the size of a domestic sheep. The second, *P. latidens* from the lower Pliocene, was somewhat larger and had horns which were slightly twisted. The genus may be placed among the Boselaphinae, of which many genera with twisted horns have been discovered in the lower Pliocene of India. The twisted horns of *Pachyportax latidens* are rather against the idea that it was ancestral to the Buffaloes, but the males of *P. nagrii* may possibly have had straight horns.

The characters in which *Pachyportax* is definitely more progressive than *Eotragus*, and by which it is allied to the Oxen and more especially to the Buffaloes are as follow: (1) the breadth of the occiput, which has an expanded squamosal shelf; (2) the slight bending down of the face on the basi-cranial axis; (3) the cross-section of the horn-core, in which we can observe the beginning of the anterior and posterior keels and the extension of the inner edge giving a section very similar to that of the horn-core of *Proamphibos* and the early Buffaloes, and which led on to the markedly triangular horn-core of the modern Buffalo; (4) the higher crowns of the molars, in which the

crescents are more compressed in an anterior posterior direction, and an expanded inner median pillar; cement is also present on either side of the enamel folds—this is a progressive character associated with the higher crowns; (5) the stouter feet in which the cannon bones have retained much of their original length, but the toe bones are shorter and stouter, thus differing from the Boselaphine Antelopes and approaching the condition seen in the Oxen.

The primitive characters which *Pachyportax* retains and which are therefore similar to those of *Eotragus* are: (1) the long brain-case, but a tendency to shortening is perhaps indicated by a V-shaped, instead of a transverse, suture between the parietal and the frontal; (2) the position of the horns directly over the orbit; (3) the deep pit at the side of the face for the reception of the facial gland; (4) the relatively narrow basioccipital with weak and but little expanded tuberosities; (5) the large size of the auditory bullae; (6) the weakness of the median rib on the outer side of the hind lobe of the upper molars.

The Buffaloes.

From now on we are in a position to distinguish the separate lineages of the Buffaloes, Oxen, Sheep and Goats, and to trace their evolution in approximate detail. We begin with the Buffaloes.

Parabos and *Proamphibos* are the earliest representatives of the true Buffalo lineage. These two genera, the former is European and the latter Indian, appeared in the lower Pliocene and continued into the middle Pliocene. *Parabos* is on the whole the more primitive, but, except for the limb-bones, the fossil remains of *Proamphibos* are the more complete. In comparison with *Pachyportax*, *Proamphibos* is more progressive in almost every way. It is about one-third larger; the occiput, of which the parietal forms the roof, is shorter, and has increased in breadth and diminished in height; the basioccipital is markedly triangular and has more prominent tuberosities; the auditory bullae are narrower; the face is broader and more bent down on the occiput; the palate is considerably thickened; the horn-cores are shifted farther behind the orbit and are more divergent, their cross-section, though similar to that of *Pachyportax*, is more expanded and convex on the inner edge; the females are still hornless; the crowns of the molars are higher and the ribs which run up the centre of the outer wall of each lobe are stronger. The pit for the reception of the facial gland retains its primitive depth in the lower Pliocene species, but by the time the genus has reached the middle Pliocene it has entirely disappeared.

The digits of *Parabos macedoniae* show a distinct approach to the Bovine type in that they tend to become shorter and stouter than those of *Pachyportax*, and the expansion of the metapodials at the distal end indicates a greater development of the toes.

Hemibos is found abundantly in the upper Pliocene of India and wandered westwards as far as Palestine. It is subject to considerable variation, but always shows a distinct advance on *Proamphibos* in the direction of the modern Indian Buffalo. Compared with *Proamphibos*, the frontal and the occipital are both broader, and the height of the occiput is less; the frontal is lengthened at the expense of the parietal, but the latter is still confined to the roof of the brain-case and is at right angles to the occipital; the frontal is arched antero-posteriorly, and on this arch the horns are situated, diverging more than in *Proamphibos* and considerably more tilted backward. The horns of the female are smaller than those of the male, and have the primitive cross-section of *Proamphibos*. In the horns of the male, the inner convexity of *Proamphibos* has become more marked and has almost changed into a third keel, so that the diameter here is greater instead of being less than it is at the two primary keels. Owing to an increase in the width of the posterior tuberosities, the basioccipital is triangular in shape. The auditory bulla is narrower. There is no facial gland.

The teeth have higher crowns with larger internal basal pillars, and with stronger ribs on the outer walls of the upper molars. Cement was probably present on the teeth, but it has not been preserved in the fossils.

Bubalus.—The earliest species which may be assigned to this genus is *Bubalus platyceros* from the Siwalik Hills of India. It seems in the main to have been of lower Pleistocene age, although some forms may have persisted until the beginning of the middle Pleistocene, which is distinctly later than the date of the *Hemibos* material.

The skull is broader in every part than in *Hemibos*. The frontal is more arched ; the parietal is more restricted, and is bent towards the occipital plane ; the facial and basicranial axes are inclined to one another ; the basioccipital has undergone a great expansion of the posterior tuberosities, so that its triangular outline is still more pronounced ; the auditory bullae are short and narrow ; there is no lachrymal fossa. In some varieties the horn-cores diverge widely, almost in the plane of the frontal, although they bend upwards towards the tips. Their cross-section is now a

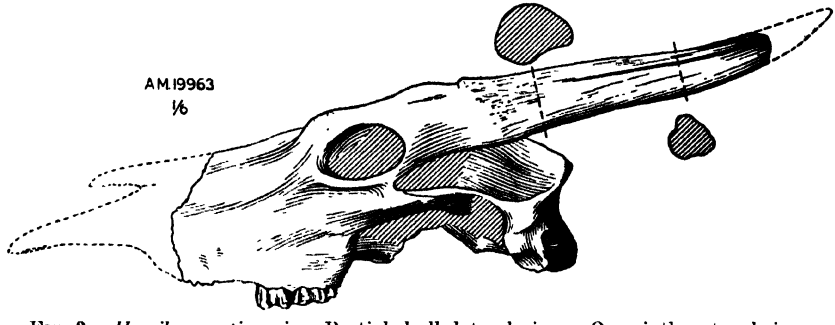


Fig. 3. —*Hemibos acuticornis*. Partial skull, lateral view. One-sixth natural size. (Copied from Pilgrim, 1939, fig. 47.)

perfect isosceles triangle with all three keels sharp, and the inner one considerably extended. The occipital is still lower than in *Hemibos*. The molars are more hypsodont, with stronger basal pillars and ribs, and have abundant cement.

Bubalus palaeindicus is probably no more than a variety of the living Indian Buffalo, and, when we know more about it, may prove to be the same as the Assam Buffalo, *B. bubalis macroceros*.

The African Buffalo belongs to the genus *Syncerus*. To judge by the short palate, which does not extend behind the teeth, and by the absence of fusion between the palatine and vomer, it is much more primitive than the preceding forms. It is also distinguished from *Bubalus* by the following additional characters : the concave facial profile ; the short and wide nasals ; the short premaxillae, either not in contact with the nasals or but slightly so ; the not very prominent orbits ; the relatively large and inflated auditory bullae ; the horn-cores are hollow only at the base.

It is possible that *Syncerus* branched off in the upper Miocene from a species of *Pachyportax* resembling *P. nagrii*, but the fossil record is silent as to its origin, which may have been in a forested area,

Oxen, Bison, Yak.

The evolutionary record of the true Oxen, Bison and Yak is much less complete than that of the Buffaloes, but there is no doubt that their development proceeded on similar lines. These are, the shortening of the parietal ; the shifting back of the

horns on the frontal; the broadening of the skull; the development of an internal keel on the horns; the heightening of the crowns of the teeth, with increasing prominence of the external ribs and of the median basal pillar; and the manner in which the limb-bones, especially the metapodials, became shorter and stouter and the toes became broader.

It is not unlikely that the Oxen branched off from the Buffaloes in the upper Miocene, and that both were derived from such a species as *Pachyportax nagrii*; but both that species and the supposed intermediate form *Perimia* found in the lower Pliocene are very imperfectly known. Furthermore, we know of no fossil species which can even approximately fill the gap between the lower Pliocene *Perimia* and the lower Pleistocene species *Bos acutifrons*.

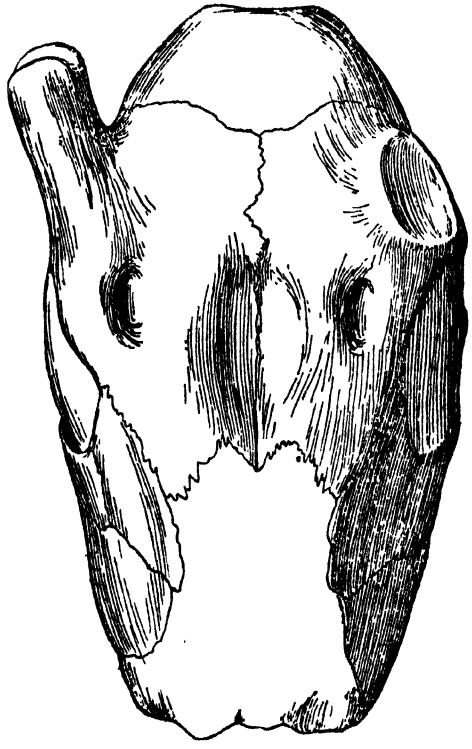


FIG. 4.—*Perimia falconeri*. Holotype viewed from above. One-half natural size. (Copied from Pilgrim, 1939, fig. 15A.)

The short lineage which began in the lower Pliocene with *Proleptobos* and is continued in the upper Pliocene by the widely distributed genus *Leptobos* affords a glimpse of the development of one of the most striking features of the oxen, namely, the deflection of the parietal from the roof of the brain-case into the plane of the occipital, and the almost complete elimination of the supraoccipital.

PERIMIA shows certain special characters of the Oxen in the widely separated horns, which are almost circular in cross-section (the only skull known is that of an adolescent), and in the absence of the arching of the frontal characteristic of the

Buffaloes. The front part of the skull is remarkably Ox-like in the absence of a lachrymal fossa, in the probable presence of a fissure between the nasal and the lachrymal, and in the separation of the premaxillae and nasals.

A striking change took place between the characters of the skull and feet of *Pachyportax* and *Perimia*, both of which are antelopine in many ways, and those of the earliest true Ox known, *Bos acutifrons*, which is found in the lower Pleistocene of India. Fortunately we have a clue to the stages which bridged this evolutionary interval in the short parallel lineage of *Leptobos*, which was widely dispersed from south-eastern Asia to western Europe.

Proleptobos, probably obtained from the lower Pliocene of the Irawaddy valley in Burma, is the earliest known member of this line,, The only skull known is hornless, and therefore that of a female. There is a distinct bending down of the rather short parietal, and still more of the supraoccipital, towards the plane of the occipital thus foreshadowing the condition in *Bos*. There is a shallow lachrymal fossa and a marked fissure between the lachrymal and nasal bones. The palate is slightly thickened ; it is not united to the vomer. The molars are moderately high ; their enamel crescents have the semi-circular shape of the modern Oxen. The face is broad in front of the orbits ; the basioccipital is triangular with expanded posterior tuberosities.

Primitive characters are, the height and narrowness of the skull behind the orbits, especially of the occiput. Special characters which distinguish this form from early *Bos* and *Bison* are the deep temporal fossae, their approach to each other, and the manner in which they open on to the supraoccipital only.

In *Leptobos* these special features are further developed. The parietal is still more shortened, and the supraoccipital is still further deflected into the plane of the occipital ; the facial gland has vanished ; the horns are approximately circular in cross-section without any trace of inner keel, though traces of two primary keels are noticeable, and in a Javan species, which is probably of lower Pleistocene age, they are slightly twisted as in certain species of *Bos*. The metacarpals are relatively slender ; compared with the length of the radius they are slightly shorter than in *Pachyportax* and more expanded at the lower end, although in both these respects they differ very considerably from the true Oxen.

Bos (including *Bibos*).—The characters of the genus are clearly displayed in the skull of the earliest known species, *Bos acutifrons* from the lowest Pleistocene of the Siwalik Hills. Both sexes appear to be horned ; the horns have increased considerably in size and the inner keel is very marked ; they have been shifted to the extreme hinder end of the frontal, stand far apart, are widely divergent, directed somewhat to the rear, and curve forward at the tips. The parietal has been shifted into almost the same plane as the occipital which forms an acute angle with the plane of the frontals. The lachrymal fossa has vanished, but there is an ethmoidal fissure, and the premaxillae do not touch the nasals. The posterior openings of the temporal fossae are narrow and, unlike those of *Leptobos*, are separated by a considerable interval. The basioccipital is triangular with large tuberosities, of which the posterior pair is much expanded transversely. The face is bent down on the basi-cranial axis at an angle of about 20°. The front premolar is considerably reduced.

Later species of *Bos* have the parietal quite in the plane of the occipital, and the horn-cores diverge at an angle of as much as 180°.

During the middle and upper Pleistocene, *Bos* was spread widely throughout Europe and Asia. The enormous Aurochs (*Bos primigenius*) inhabited the forests of Europe and was gradually exterminated by hunters. Its last refuge was in Poland, where it did not become extinct until the 17th century. Drinking-cups over six feet long made from Aurochs' horns were in existence until comparatively recently.

Bos namadicus, a close relation of the Aurochs, is known from fossil remains found in the middle Pleistocene alluvial deposits of various rivers of peninsular India.

Wild cattle exist today in the Gaur (*Bibos gaurus*) found in the hilly parts of India, and in the Bantin (*Bibos banteng*), which lives in Java and the Malay Peninsula, The former stands six feet high or more at the shoulder. The Gayal (*Bibos frontalis*) is a partly domesticated race of the Gaur.

Various breeds of domesticated oxen are found throughout the world; the most remarkable is the humped ox (Zebu) of India, a breed of unknown origin which may be derived from *Bibos banteng*.

The Yak (*Bos grunniens*) of Tibet is closely related to the Oxen, but differs from them in the possession of fourteen pairs of ribs. It has been made the type of a separate genus, *Poëpgahus*. No annectant forms are known.

Bison differs from *Bos* in the parietals being very nearly in the same plane as the frontal, and inclined at a considerable angle to the plane of the occipital. The skull itself, especially the occiput, is very broad and low; the basioccipital somewhat approaches a quadrangular shape, with the posterior tuberosities but little expanded laterally; the auditory bullae on either side of it are large and inflated. The horns are far apart and situated not far behind the orbits; they diverge at an angle of about 180°, and vary from triangular to circular in cross-section. *Bison sivalensis* is probably an upper Pliocene species, and the earliest member of the genus.

The Bison is the only instance of a true Bovine migrating from Asia to North America, where it is represented by no less than seven different species distributed throughout the Pleistocene, and ranging from Alaska to Florida.

It is probable that, in the middle Pliocene, the lines leading to the Oxen, Bison and Yak, branched off from a common ancestor.

The European Bison, or Wisent, was common in the forests of central Europe during the early part of the Christian era, but it was hunted to extinction, until, just before the present war, it only survived in a special preserve in Poland.

Sheep and Goats.

The Sheep and Goats, together with the Gazelles, the Caprine Antelopes *Rupicapra*, *Budorcas* and *Nemorrhaedus*, and the Musk Ox and its ancestors, have been separated from the Oxen and so-called Bovine Antelopes as a special section of the Bovidae termed Aegodontia. They are characterized by narrow teeth with median ribs on the outer lobes of the upper molars, and with smooth enamel on the inner lobes of the lower molars. There is either a lachrymal fossa, or a fissure between the lachrymal and nasal bones. The Gazelles, first known in the middle Miocene, are the earliest, as they are the most primitively constituted of the group. They are unlikely to have any connexion with *Eotragus*, the first horned Boodont known, and the origin of both *Eotragus* and *Gazella* must be sought in some as yet unknown ancestral genus in the lower Miocene or upper Oligocene, which, at a still more ancient epoch, evolved from the tragulid genus *Gelocus*. The Gazelles have persisted to the present day, but the Sheep and Goats may have branched off from an early Gazelline at least as early as the middle Miocene.

A great gap exists between this hypothetical form and the true Sheep. There is another gap between this form and the first Goat, *Tossunoria*, which is found in the lower Pliocene of China. The gap in the ovine line is partially filled by a short lineage (*Oioceros*), which may not be directly ancestral to the true Sheep (*Ovis*), but which we may employ, as we did *Leptobos* among the Oxen, to illustrate the changes through which the ovine ancestor passed on its course of development into true Sheep.

Gazella.—The genus abounds in the lower Pliocene deposits of Europe and Asia, but its remains are first found in the upper Miocene of Europe and India. The fragmentary fossil remains of these very early Gazelles consist merely of isolated horn-cores and teeth, and differ from the remains found in lower Pliocene deposits

only in their smaller size. They cannot be claimed as direct ancestors of the Sheep and Goats since the contemporary *Oioceros* is much more closely related to the Sheep.

It is unlikely that *Eotragus*, which is ancestral to the Oxen and to the Bovine Antelopes, gave rise either to the Gazelles or to the Sheep. Some unknown form of the middle Miocene may have been ancestral both to the Gazelles and to *Oioceros* and the common ancestor of *Eotragus* and the Gazelles, possibly a hornless form, is likely to be recognised one day in the lower Miocene or even earlier. We may, however, consider *Gazella* as presenting many features which must have characterized the hypothetical ancestor of the Sheep and Goats.

The Gazelles of the lower Pliocene have a relatively narrow skull with a long face, the frontal being only slightly longer than the parietal. The frontal gradually bends down on the parietal, as a beginning of the extreme bend which was to take

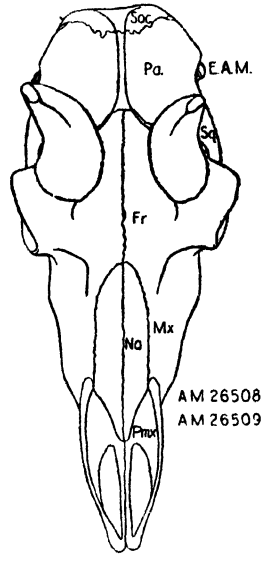


FIG. 5.—*Oioceros* (?) *grangeri*. Diagram of skull viewed from above. One-fourth natural size. (Copied from Pilgrim, 1934, fig. 4.)

place later in the true Sheep and Goats. The horns are circular, or slightly compressed, in cross-section ; they stand directly over the orbits, and are only slightly divergent ; the females are hornless. There is a deep lachrymal fossa, and a fissure between the nasal and the lachrymal bones. The basioccipital is narrow but more expanded behind ; the auditory bulla is relatively large. The teeth are rather low-crowned, and the upper molars are longer than broad, although the first molar is rather square On the outer side the median rib of the posterior lobe is weak (in the living Gazelles both lobes are practically flat). The limbs are long and slender, the cannon bone being as long as the radius ; a vestige of the lateral digit persists.

In the later and living Gazelles, many of these characters have undergone some slight change in the direction of the Sheep and Goats. Thus the teeth are hypsodont, and the female has developed horns, though these are usually much smaller than those of the male. The auditory bulla is more flattened, but still retains its triangular shape.

Oioceros.—In the upper Miocene species *Oioceros grangeri* and *O. noverca*, both from China, we have the earliest occurrence of the true Sheep type. The skull is extremely broad at the orbits, and narrow towards the front. There is a deep lachrymal fossa. The parietal is a little shorter than the frontal. The horns in the male (the females are hornless) are slightly twisted in an anti-clockwise direction for the right horn, and clockwise for the left. The basioccipital is sub-triangular with a convex surface. The bulla is small and short. The teeth are rather low-crowned. The median rib on the anterior lobe of the upper molars is not very prominent, and on the posterior lobe is practically absent. The premolar series is somewhat reduced. No limb-bones have yet been found.

Oioceros proaries and *O. kuhlmanni* were both found in the lower Pliocene deposits of Samos; the former which is hornless, is probably the female of the latter. The genus itself is widespread in beds of the same age in northern Asia, Persia and Europe, but the two species found on Samos are much more advanced in the direction of the true Sheep than any of the others, so much so, indeed, that *Oioceros kuhlmanni* was first described as a species of *Ovis*. The following characters show clearly that these two forms are more progressive than those from the upper Miocene of China.

The angle which the face makes with the parietal is much greater, nearly 90°. The parietal itself is much shortened, and the occipital is narrower. The horns are longer, more twisted, and much inclined backwards, almost in the plane of the face, and are situated wholly behind the orbits.

In certain features, however, the advance towards *Ovis* is slight. Thus, the teeth have hardly increased in height, and the median rib on the outer wall of the anterior lobe of the upper molars is still plainly visible. The premolars are not noticeably reduced. The nasals have retained their primitive length and slenderness; the basioccipital is in the same plane as the basisphenoid and has little tendency to assume the broad quadrate shape of *Ovis* and *Capra*. The lachrymal fissure still persists. Another primitive feature is the presence of a long vestigial lateral digit. Whether the cannon-bones were more advanced, that is to say, whether they were shorter and broader, is not yet known.

Ovis.—The presence of a true Sheep in the upper Pliocene deposits of Senèze France, has been recorded, but the specimens have not yet been described or figured Another true Sheep of early date is *Ovis shantungensis* from the Nihowan beds of China.

Several specimens of Sheep have been described from beds of Pleistocene age, and most of them have been referred to living species. It is possible that they have descended from one of the species of *Oioceros* described above.

The most striking of the characters in which *Ovis* has progressed beyond even the most advanced species of *Oioceros* are—the greatly increased size and greater torsion of the horns; their greater divergence and triangular cross-section; the general presence of horns in the female, though as a rule the horns are small and upright, and in some living species the females are hornless; the horns are generally very large and form an open spiral which curves backwards, downwards and forwards, and then bends inwards at the tip, they have also been shifted far behind the orbits; the parietal is much shorter and stands at a right angle to the frontal; the nasals and premaxillae are shorter, which takes away the sudden narrowing of the face characteristic of *Oioceros*; a lachrymal fossa is retained, but the fissure has been obliterated, and the premaxillae do not articulate with the nasals. The occipital is narrower; the basioccipital is square in outline, concave on its ventral surface, broader in front than behind, and forms an obtuse angle with the basisphenoid.

The teeth are very high-crowned and the median ribs on the outside of each lobe, of the upper molars have completely disappeared. The premolars are further reduced.

The limbs are still long and slender, but the cannon bones are much stouter

than in the Gazelles. The vestige of the fifth metacarpal is seen as a small knob on the outer side of the upper end of the cannon bone, and, in the domesticated races at least, is often missing.

Fossil remains of Pleistocene Sheep are known from the Norfolk Forest Bed and also from various parts of Germany and France; they are more or less closely related to the wild Sheep of to-day.

Wild Sheep are known from all parts of the northern hemisphere, though they are now much scarcer than they were during the Middle Ages. For example, the European Mouflon (*Ovis musimon*), the smallest of the wild species, is now restricted to the mountains of Corsica and Sardinia, whereas it formerly occurred in many parts of the continent. In this species the face-glands are small, and the female is very often hornless. The Asiatic Mouflon (*Ovis orientalis*) is found in the Elburz range of northern Persia, in Armenia, and in the Taurus range of Asia Minor; it is the probable ancestor of the so-called Turbary Sheep.

Other wild Sheep are the Urial (*Ovis vignei*), which ranges from northern Tibet, through Russian Turkestan and Afghanistan to the Salt Range in N.W. India. The Argali (*Ovis ammon*) is the largest of all living Sheep; it may stand as much as four feet high at the shoulder, and its range extends from Bokhara to Tibet, Mongolia, and eastern Siberia. Marco Polo's Sheep (*Ovis polii*) has horns of great length—the record is some 75 inches—which are relatively slender and twisted in a more open spiral than are those of the species previously mentioned; its typical locality is the Pamirs. The African Sheep or Arui (*Ovis lervia*), which is restricted to North Africa, is sometimes referred to a separate genus as *Ammotragus lervia*; it has no face-glands, and the female has larger horns than are usual in the other species.

The Bharal (*Ovis nahoor*) is often referred to the genus *Pseudois*, and is regarded as a link between the Sheep and the Goats. In particular, the basioccipital is narrower in front than behind, a character which usually distinguishes the Goats from the Sheep. The face-glands are absent. This species lives on the Tibetan plateau and the adjacent mountains, and never descends below 10,000 feet, even in winter.

Remains of domesticated sheep have been found in the Swiss Lake-dwellings, and in Bronze Age deposits in Turkestan. Domestic sheep may be recognized by their lighter and more porous horn-cores, in which the spongy bone of the interior is developed at the expense of the compact external layer. They are classed under the name *Ovis aries* L., but this is almost certainly a collective species comprising animals of widely differing origin. The probable descent of the Turbary Sheep from *Ovis orientalis* has already been mentioned, and there is good reason to believe that some foreign breeds have been derived from the Argali, and that some of the prehistoric domestic sheep of Turkestan may have had their origin in *Ovis vignei*.

Goats.—The Goats, generally regarded as comprising the two genera *Capra* and *Hemitragus*, are very closely allied to the Sheep. They have a more southerly range than the latter, which is probably why they never reached the New World by way of the narrow Behring Strait, which was once dry land, and which is believed to have been the route followed by Asiatic mammals migrating to America.

The Goats are distinguished from the Sheep mainly by the horns, which are more compressed and which are twisted in a clockwise spiral; by the absence of face-glands, and consequently of the pit which lodges the glands; by the presence of an ethmoidal fissure; and by the different shape of the basioccipital, which, though broad and concave as in the Sheep, differ in being narrower in front than behind. The back teeth, too, are not so high-crowned, and the cannon bones are shorter. Externally they are distinguished by the presence of strongly odoriferous glands under the tail of the male Goat, and by their bearded chins.

Tossunoria from the lower Pliocene of eastern China is the earliest form which may be regarded as ancestral to the Goats, especially to *Hemitragus*. Since it is

a contemporary of those European species of *Oioceros* which are closely related to the Sheep, and since it is only slightly later in date than the Chinese species *Oioceros grangeri* and *O. noverca*, it seems obvious that we must seek for the separation of the lineages of the Sheep and Goats in the lower or middle Miocene. Very probably the same hypothetical ancestral Gazelle gave rise to both, but there is at present no fossil evidence to support this view.

Tossunoria is known only by an imperfect skull from China. The horn-cores are large and bend backwards as in *Hemitragus*, and have a sharp keel in front. Apart from this, they are oval rather than pear-shaped in cross-section and seem to be situated well in front of the fronto-parietal suture. The occipital is extremely low. The face is bent down on the parietal.

The base of the skull does not resemble that of the living Goats. The basioccipital is narrow, and the two pairs of tubercles are united by two longitudinal swellings enclosing a central groove. The auditory bullae are large ; their structure resembles that of the lower Pliocene Gazelles and is very different from that of *Oioceros*, or of the Recent Sheep and Goats. The dentition is unknown.

Sivacapra is founded upon a skull from the upper Pliocene of India. It resembles *Tossunoria* in many ways, and, like that genus, finds its nearest living relative in

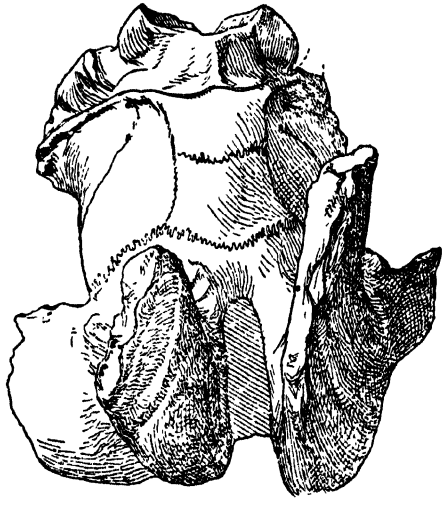
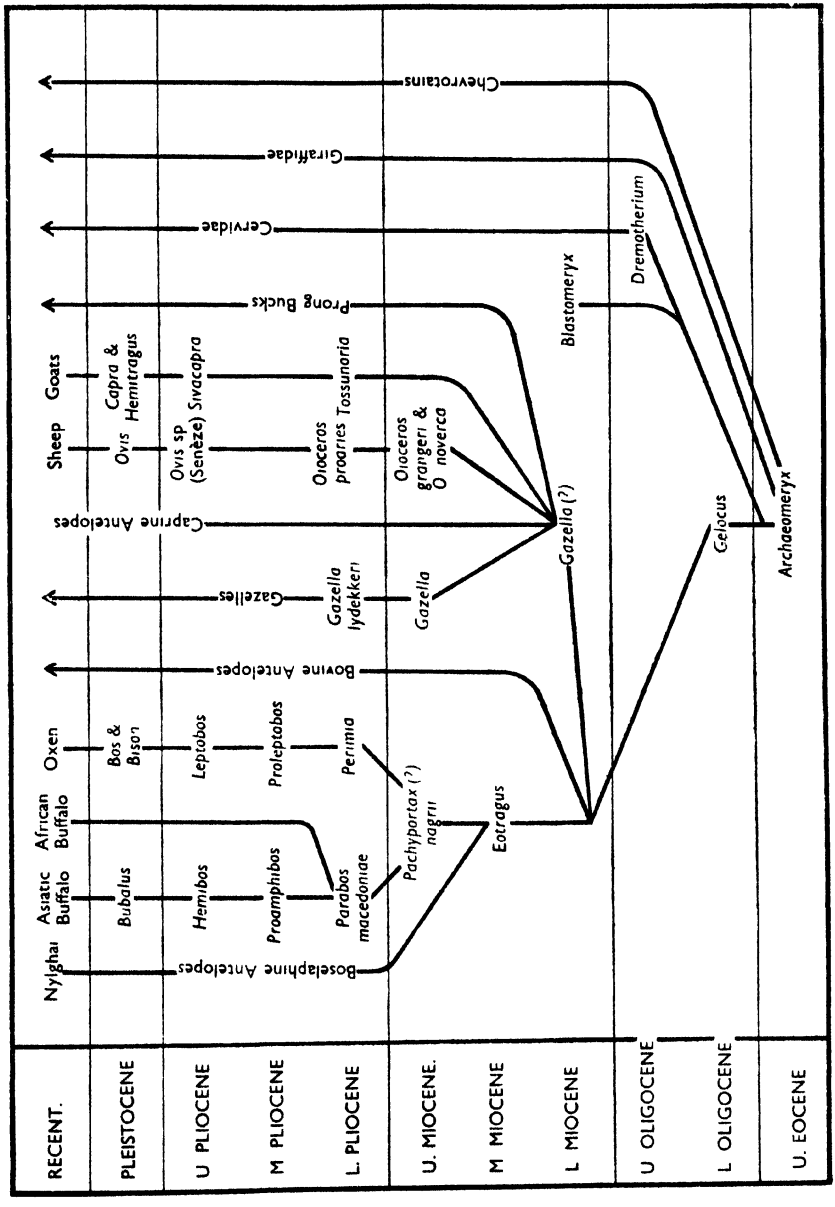


Fig. 6.—*Sivacapra sivalensis*. Brain-case and horn-cores viewed from above. One-half natural size. (Copied from Pilgrim, 1939, fig. 4.)

the Tahr (*Hemitragus*). The horns are more pear-shaped in cross-section but are flattened on their inner surfaces. The face is bent down at right angles to the parietal. The brain-case is narrower, although the occipital is low and broad, The large auditory bullae, and the shape of the basioccipital are very similar to those of *Tossunoria*, but *Sivacapra* has advanced beyond that genus in the shortening of the parietal. The median hollow on the ventral surface of the basioccipital is broader than the corresponding groove in *Tossunoria* ; in this respect also, there is an advance towards the characters of the modern *Capra*.

Capra—Many specimens of this genus have been recorded from the Pleistocene deposits of Germany. They are closely related to living species, or to *Hemitragus*. The most striking progressive features are the broader brain-case ; the higher and


EVOLUTION OF THE PECORA.
RECENT.
PLEISTOCENE
U PLIOCENE
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U OLIGOCENE
L OLIGOCENE
U. EOCENE
Nylghai
Asiatic Buffalo
African Buffalo
Oxen
Sheep
Goats
Boselaphine Antelopes
Bubalus
Hemibos
Proamphibos
Parabos macedoniae
Pachyportax (?) nagrii
Bos & Bison
Leptobos
Proleptobos
Perimia
Eotragus
Ovis
Capra & Hemitragus
Ovis sp (Senèze)
Sivacapra
Oioceros prearies
Tossunoria
Oioceros grangeri & O noverca
Bovine Antelopes
Gazelles
Gazella lydekkeri
Gazella
Gazella (?)
Caprine Antelopes
Prong Bucks
Blastomeryx
Cervidae
Dremotherium
Giraffidae
Chevrotains
Gelocus
Archaeomeryx

narrower occipital ; the further shortening of the parietal, not indicated in *Hemitragus*; the narrower and smaller bullae ; and the flat, expanded basioccipital. The dentition is unknown.

Various remains of Goats have been found in the Pleistocene of Europe. The best known of these is *Capra prisca* from Hungary ; it is related to the living Ibex. *Capra savini* from the Norfolk Forest Bed seems to be nearest to the Pallas Goats, or Tur. The German species described under the names *Hemitragus stehlini* and *H. kunbergii* are related to the Tahr.

The species of wild Goat now living include the various species of Ibex (*Capra ibex, C. pyrenaica, C. siberica*) which are distributed throughout the high mountain chains of Europe and Asia from the Pyrenees to Mongolia and eastern Siberia. *Capra walii*, which lives in the mountains of Abyssinia is the southern representative of the Siberian Ibex. All these species have very long, compressed, scimitar-like horns which sweep boldly backwards, and which measure from two to three feet in length along the curve.

Capra aegagrus has horns resembling those of the Ibexes, but they are longer, measuring up to four feet in length, and have bold, widely separated knobs on the front. It ranges from the mountains of south-eastern Europe to those of south-western Asia, from the Caucasus to Persia and Baluchistan. It was formerly abundant on the islands of the Grecian archipelago, from many of which it has now been exterminated.

The Markhor of Kashmir (*Capra falconeri*) is the handsomest of the wild Goats. Its horns are twisted either into an open spiral of about one and a half revolutions, or else into a tight spiral of two or three complete turns ; there are intermediate forms. The better specimens have horns which are over three feet long in a straight line, and measure fourteen inches or more in basal girth.

There are three species of *Hemitragus*, namely, *Hemitragus jemlahica*, which is found in the outer and middle ranges of the Himalayas, *H. jayakari* living in Oman, and *H. hylocrius* which inhabits the Nilgiri hills and other mountain ranges of southern India. They all agree in the possession of short, stout, compressed horns, sharply keeled in front, which almost touch at the base, curve backwards, are moderately divergent, and are up to fifteen inches long. No true Goat ever reached America ; the so-called Rocky Mountain Goat (*Oreamnos*) is a Caprine Antelope allied to the Chamois (*Rupicapra*).

Domesticated goats are believed to have originated in part from the Markhor, which interbreeds with the tame goat, and in part from *C. aegagra*. The latter probably interbred with the descendants of the Pleistocene *C. prisca*. Neither *Capra siberica*, nor the European Ibexes, nor *Hemitragus*, appears to have any share in the production of the modern domesticated goats.

Literature.

There was no list of literature accompanying the MS., but very full references will be found in Dr. Pilgrim's monograph, " The Fossil Bovidae of India ", *Palaeont. Indica*, Calcutta, N.S., **xxvi**, Mem. 1, 1939.

The illustrations are direct copies of the figures in,

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to which full acknowledgements are made

Six Specimens of Lyomeri in the British Museum (with notes on the skeleton of Lyomeri).*

By V. V. TCHERNAVIN. (From the Department of Zoology, British Museum, Natural History.)

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* Since this paper was in the printers' hands, I received, through the kindness of Dr. Å. V. Tåning of the Marine Biological Station in Charlottenlund Slot, a number of specimens of *Eurypharynx* for study. Anticipating my account of this study, I want to note here that the course of the cephalic nerves and of the branchial arteries shows, that *all the six visceral clefts of* Eurypharinx *are branchial clefts, and that the ventral elements of the hyoid arch are completely missing in this fish* (see pp. 312, 338 and 339 *of this paper*). In both these respects *Eurypharynx* is unique among bony fishes.

A brief account of this work is published in *Nature*, vol. 158, p. 687, November 9, 1946; and a fuller account is ready for publication.

I.—Description of the Specimens of Lyomeri preserved in the British Museum

1. *Two Specimens of* Saccopharynx.

Of the known specimens of *Saccopharynx* only thirteen have been recorded for certain since, 120 years ago, Mitchill (1824) described the first specimens of this genus. Mitchill's specimen, as well as those described by Harwood (1827) and Girard (1895), were not preserved, and among those ten which have probably been preserved, at least five are known to be in poor condition.* When Bertin (1932*a*, 1934, 1938) revised the Lyomeri, he saw five specimens of *Saccopharynx*, of which one he recognized as belonging to a species previously described, one he described as a new species, and three he could not determine at all. Thus the *five species* of *Saccopharynx* which Bertin describes, are based on the actual study of *two specimens* only, and *his three new species* are based on the study of a *single specimen* ; Bertin's creation of the two other new species is the result of an examination of figures found in earlier papers.

This shows the scarcity of our knowledge of *Saccopharynx*, and that every specimen of this amazing genus is worth investigating. A list with some particulars of all *Saccopharynx* recorded in the literature is given in the table on pp. 290, 291.

The two specimens of *Saccopharynx* preserved in the British Museum are of special interest as they are the first specimens of Lyomeri preserved ; everyone working on this group refers to these specimens, but it seems that nobody knows what they really are.

The history of all specimens of Lyomeri known up to 1884 has been described with great precision by Gill and Ryder (1884). This encouraged later writers on Lyomeri to give the "history" of these fishes by copying Gill and Ryder's data. Thus, mainly those details not mentioned by Gill and Ryder concerning the fate of the two specimens of the British Museum are given here.

Johnson's specimen of Saccopharynx.—There is no original label from the sender. Label of the British Museum : *Saccopharynx flagellum*, Madeira, presented by J. Y. Johnson, Esq. 11.6.43. Johnson determined this specimen as *Saccopharynx ampullaceus*, published its description (Johnson, 1862), and sent the *Saccopharynx* to the British Museum, where the specimen was registered on June 4th, 1861, under No. 3. No specific name was given in the Register. At that date Dr. A. Günther was in charge of the fishes in the Museum. His curiosity was more attracted by the fish distending the *Saccopharynx's* stomach than by the *Saccopharynx* itself. The *Saccopharynx* was dissected and its prey described (Günther, 1862, p. 342). It proved to be a new genus and species (*Halargyreus johnsoni* Günther). The extraction of the 9-inches-long, stout *Halargyreus* (Günther, 1887, p. 257) from the belly of the *Saccopharynx*, whose whole trunk was only 6 inches long (Günther, 1870, p. 22), could not be done without major injury to the *Saccopharynx*. After being dissected the *Saccopharynx* was apparently not touched for 26 years. Günther mentions this specimen in his Catalogue (1870, pp.19, 22, 23), but from his description it is clear that he was satisfied with Johnson's (1862) data, and did not examine the specimen himself. The absence of opercular bones and the unique condition of the ventral part of the hyoid arch, which were overlooked by Johnson, are not mentioned by Günther ; the filaments of the lateral line, the dorsal filaments on the posterior part of the tail, and the caudal organ escaped Johnson's attention and they are also missing in Günther's description ; on the other hand, Johnson's erroneous descriptions of a toothless palate and of a single nostril on each side are repeated by Günther. The only original thing in Günther's description was the mistaken renaming of this specimen as *S. flagellum*.

* Bertin (1938) determined as larvae of *Saccopharynx* 123 specimens collected by the 'Dana' Expedition. It seems, however, that this determination may not be exact. See p. 301.

However, being later sharply engaged by Gill and Ryder (1883, 1884) in polemics concerning *Saccopharynx*, Günther (1887) re-named Johnson's specimen back to *S. ampullaceus*, and found that the condition of the specimen had markedly deteriorated. Thus, he remarks (p. 258) that the teeth of the jaws 'have now almost entirely disappeared', and from the following text it is clear that no teeth were left in the specimen. Günther further dissects the specimen. He describes (p. 259) and figures (pl. lxvi) two vertebrae of the middle of the trunk, describes the cartilages supporting the gill arches, 'hidden below the skin', and the anterior rays of the dorsal fin which 'become visible only by dissection'.

Thus an intensive dissection of Johnson's specimen started. When such an extraordinary and fragile specimen as *Saccopharynx* is preserved semi-dissected, its condition deteriorates rapidly. Even a careful handling brings further injury to the specimen; and the inquisitive mind of any one who handles it cannot resist the temptation of somewhat enlarging the dissection in order to investigate the puzzling structures still hidden under the tissues. This has presumably happened to Johnson's specimen of *Saccopharynx*. There are indications that Boulenger (1904*b*, p. 603), Zugmayer (1911, p. 92), and Regan (1912*a*, p. 348) have studied it. Boulenger and Regan describe such parts of the fish as could not be seen without dissection (the hyomandibular, the quadrate and their junction, the bones composing the lower jaw, bones of the roof of the neurocranium). But the state of preservation of the specimen suggests that even more scientists have examined it though there are no published results of their work.

Bertin (1934, pp. 45–47) chose this specimen as the type of his new species *S. johnsoni* though he had not seen it.

It is not unusual that those who study a specimen do not leave any published trace of their endeavours, while those who describe and name it have no time or opportunity to examine the specimens they describe.

During the present examination no new dissection was made, but the handling of the fragile fish, when studying it under the microscope, could not be done without further injury to it.

The present state of preservation of Johnson's specimen.—The specimen is dissected along the right side, so that the whole cavity of the body is open. The stomach is also dissected. Only a small portion of the intestine is present; the liver, genitals and kidneys are missing. The heart and pericardium are dissected; the ventral aorta, the efferent branchial arteries, and the large veins entering the *sinus venosus* can still be recognized. The cranium is separated from the trunk, and from the first vertebra. Only the roots of the cranial nerves are present. The shoulder girdle of the left side is removed (preserved in a separate tube). The integuments and muscles are almost entirely removed from the cranium, from the suspensory elements and partly from the jaws. The roof of the skull is broken, but no bones are missing. The suspensorium is broken in the middle of the bar, so that its lower part has become 'capable of being swung in all directions'; which Boulenger thought a natural condition of Lyomeri (1904*b*, p. 603). The dorso-lateral muscles are dissected in several places so as to make possible a study of the vertebrae. The greater part of the fin-rays are missing. The skin and the muscles at the anterior part of the dorsal fin are dissected and the fin is damaged; it is impossible to count the rays in front of the vertical line of the vent. It can be seen that the first ray of the anal fin is about 8 mm. behind the anus. 140 vertebrae altogether were counted in this specimen but there is no urostile, and it is possible that three or four vertebrae are lost. The anterior visceral arch is under the 11th–12th vertebra, the shoulder girdle under the 15th, the posterior end of the heart under the 17th, the anus under the 34th; 106 vertebrae were counted in the tail. The dorsal filaments are situated above the 89th and 101st vertebrae of the tail.

List of specimens of *Saccopharynx*

	Date of capture.	Collected by :	Locality.	Depth or length of cable in M.	Total length of specimens in cm.	Sex.	First described by :
1	1824 ?	Capt. H. Coffin	52° N., 30° W.	0	184	♀	Mitchill, 1824
2	1826	Capt. Sawyer	62° N., 57° W.	0	137	—	Harwood, 1827
3	March 1861	—	off the coast of Madeira	0	81	—	Johnson, 1862
4	not known	—	—	--	29	—	Günther, 1870
5	18.9.1886	'Albatross' st. 2717	38° 24′ N., 71° 13′ W.	about 800 depth	about * 120	--	not described
6	1894	—	off the coast of Portugal, 9 m. from R. Tage	0	95	—	Girard, 1895
7	16.4.1911	'Princesse Alice' st. 3131	between Madeira & Azores	0–4500 cable ?	15	—	Roule & Angell, 1933
8	29.7.1913	'Margrethe' st. 1005	52° 22′ N., 24° 56′ W.	2,000–3,000 cable	105	♀	Jespersen, 1916
9	9.11.1921	'Dana' st. 1165 VIII	12° 11′ N., 35° 49′ W.	3,000 cable	23	—	Bertin, 1934
10	11.1.1922	'Dana' st. 1203 X	7° 30′ N., 79° 19′ W.	3,500 cable	—	—	Bertin, 1934
11	4.9.1928	'Dana' st. 3549, IV	7° 16′ N., 79° 30′ W.	4,000 cable	90	—	Bertin, 1934
12	28.1.1929	'Dana' st. 3655, I	33° 39′ S., 159° 00′ E.	1,000 cable	138	—	Bertin, 1934
13	11.4.1931	Bermuda Expedition	32° 12′ N. 64° 36′ W.	about 500 depth	140	—	Beebe, 1932

* Judging from the drawing.

Beside the 13 specimens listed here two more doubtful specimens of *Saccopharynx* have been mentioned in the literature :

(1) Goode & Bean (1882, 1895) refer to a mutilated specimen of *S. flagellum* secured by the 'Blake' in 35° 44′ 40″ N., 74° 40′ 20″ W. at a depth of 898 fathoms. According to Gill & Ryder (1884, p. 65) this specimen is an *Eurypharynx*.

recorded in the Literature.

First figured in :	Preserved in : condition.	First named :	Probably is :
—	Not preserved	*Saccopharynx* (= *Stylophorus*)	*S. flagellum*
Harwood, 1827	Not preserved	*Ophiognathus ampullaceus*	*S. ampullaceus*
Günther, 1887 : made a figure	British Museum : dissected	*S. ampullaceus*	*S. ampullaceus*
From these two specimens	British Museum : poor	*S. flagellum*	*S. ampullaceus*
Goode & Bean, 1895	U.S.N. Museum : not known	*S. flagellum*	*S. flagellum* *
Girard, 1895	Not preserved	*S. ampullaceus*	*S. ampullaceus* ?
—	Monaco ? : poor	*S. ampullaceus*	*S. ampullaceus* ?
Jesperson, 1916	Copenhagen : satisfactory	*S. ampullaceus*	*S. flagellum*
—	Copenhagen : good	Not determined	Description unsatisfactory
—	Copenhagen : poor	Not determined	Description unsatisfactory
—	Copenhagen : dissected	Not determined	Description unsatisfactory
Bertin, 1934	Copenhagen : good	*S. schmidti*	*S. schmidti* ?
Beebe, 1932	New York Zool. Soc ? : good	*S. harrisoni*	*S. harrisoni*

(2) Hjort gives a sketch of a specimen of Lyomeri recalling the *Saccopharynx* (Murray & Hjort, 1912, fig. 83). The specimen was found (Murray & Hjort, 1910) in 34° 59′ N., 33° 1′ W.; sounding depth 2615–2865, the 'Michael Sars', st. 53, 8.4, 1910, total length of the specimen 20 cm. Hjort writes that this fish belongs to a *new genus*, but gives it no name. (For more detail of this specimen see p. 298.)

An examination of the skin shows that some papillae along the lateral line are still present, and confirms Johnson's statement that there is no trace of the long dorso-lateral filaments along the sides of the dorsal ridge (such as described by Mitchill in his *S. flagellum*) ; but the basal parts of two dorsal filaments in the posterior part of the caudal region are still there. The latter were overlooked by Johnson and Günther. These filaments are indubitably similar to those described and figured by Harwood in his *S. ampullaceus*, and those described by Bertin, as found exclusively in his *S. schmidti*. The tip of the tail is broken off, and thus the caudal organ, described in this specimen by Zugmayer (1911, p. 92), is lost.

Owing to the poor condition of the specimen, only a few measurements could be taken. Comparing the measurements with those obtained by Johnson in 1861, one has to bear in mind that Lyomeri, preserved in spirit for a long period of time, shrink noticeably (Bertin, 1934, p. 35). Johnson gives the following dimensions of his specimen :—Total length 32 inches (812 mm.) ; from the tip of the snout to the gill opening 3⅛ inches (79 mm.) ; predorsal space about 7½ inches (108 mm.) ; the space from the tip of the snout to the vent 8½ inches (216 mm.) ; length of the jaws 2⅛ inches (54 mm.). Günther, copying Johnson's figures, gave by mistake the length of the jaw 2½ inches. Bertin (1934, Table VII) calculating the proportions of this specimen, used not the original and correct figures of Johnson, but the wrong figures given by Günther. The measurements taken now are :—Total length 770 mm. (the tip of the tail is missing) ; the length from the tip of the snout to the anus 185 ; the length of the lower jaw 55 ; the length of the suspensorium 54 ; the length of the cranium 19 (including the ' rostrum ', which is 7 mm. long) ; the breadth between the outer edges of the two sphenotics 12 ; the diameter of the eye-ball 3 mm.

The fish has died with the anterior part of its dorso-lateral muscles contracted, lifting upwards the head and six anterior vertebrae (text-fig. 5). The 6th and 5th vertebrae gradually change their horizontal position to a vertical one, and the four anterior vertebrae are turned up vertically at a right angle to the posterior part of the body. In such a position the suspensorium stands nearly vertically, and the mouth and the throat can be widely opened. The fish has apparently died in about the same position as Girard (1895) figured his specimen of *Saccopharynx*.

Girard's figure is of interest ; though perhaps not drawn by an expert draughtsman, it is made with great care from a fresh specimen, brought alive to the shore, and the figure shows what the naturalist really saw. However, this figure is completely neglected by later scientists.

Just the contrary happened to Günther's figure (1887, Pl. lxvi) made in 1887 from the specimen collected by Johnson in 1861, *i.e.*, twenty-five years after this *Saccopharynx* had been dissected, and its prey (shown in this figure as visible inside the *Saccopharynx* through the thin tissues of its abdomen) had been removed. This figure of Günther's is reproduced in nearly every scientific and popular work where the Lyomeri are mentioned. Nevertheless, this figure is but a restoration, and is exact only so far as Günther could remember it after a quarter of a century had passed since he had dissected it. The teeth are drawn from another specimen (Günther, p. 258) ; the anterior part of the body is shown much less upturned than it really is. The figure agrees better with Günther's description of *Saccopharynx* than with the specimen which it represents. Thus, contrary to what is found in the specimen, it has no lateral line, no filaments on the dorsal side of the tail, no caudal organ, and the free membrane surrounding the gill opening is not shown.

It is regrettable that Bertin (1934, pp. 45–47) described a new species of *Saccopharynx* from this imperfect drawing without consulting the specimen from which it was made.

Phillips' specimen of Saccopharynx.—Little is known about the origin of the second specimen of *Saccopharynx* preserved in the British Museum. There is no label

from the sender. The British Museum label is : ' *Saccopharynx flagellum*, presented by Mrs. Phillips '. There is no registration number, and no trace of this specimen could be found in the Register. The specimen is first mentioned in Günther's Catalogue (1870, p. 22). In 1887 (p. 257) Günther writes that the origin of this specimen is unknown, and that it has much shrivelled ' having been preserved for a long time '. Günther gives its dimensions. Body 3 (76 mm.) and the tail 8½ inches (216 mm.) long, length of the jaws 13½ lines (28 mm.). On p. 258 Günther describes its teeth in some detail.

This *Saccopharynx* is in poor condition ; apparently at one period the spirit evaporated, for the specimen has dried and shrunk. Its body and tail are twisted ; the tail is broken and its tip is missing ; the rostrum is bent down and backwards. The jaws and their teeth are in comparatively good state, a few filaments of the lateral line can be well seen, and there is still a dorsal filament in the posterior part of the tail similar to those figured by Harwood in his specimen. There is no sign of dorso-lateral filaments such as were found in Mitchill's *Saccopharynx*.

The Systematic Position of the Specimens of Saccopharynx *preserved in the British Museum.*

The systematics of Saccopharyngidae are somewhat confused because the types of the first two species described (*S. flagellum* and *S. ampullaceus*) were not preserved, while their descriptions were not precise. Only *S. ampullaceus* was figured, and its figure is rather poor. Thus, there is no means of making quite certain what fishes Mitchill and Harwood had in hand when they described their species. Cuvier (1829, p. 355), Johnson (1862, p. 279), Gill and Ryder (1884, p. 64) and Goode and Bean (1895, p. 157) hold that Mitchill's and Harwood's specimens are different species, while Günther (1887, pp. 260, 261) came to an opposite conclusion. Günther's authoritative opinion was adopted by later writers.

However, from Mitchill's and Harwood's data it seems most probable that they described distinct species. Later findings confirm this opinion.

1. In *S. flagellum* numerous dorso-lateral filaments are present ; according to Mitchill about 50 on each side—' all the way from the head down to the back of the tail ' (Mitchill, 1824, p. 83).

In *S. ampullaceus* no such dorso-lateral filaments are found, but *a few minute filaments take their growth from the posterior part of the dorsal fin* (Harwood, 1827, p. 55). This is confirmed in Harwood's figure, where four such dorsal filaments are shown. More recent material shows that specimens of *Saccopharynx* with both kinds of filaments are found, and that this character is of specific value.

2. The tail of Mitchill's specimen is relatively much longer and the body much shorter than in Harwood's specimen. The length of the body from the tip of the snout to the anus is 19 per cent. of the total length in the former specimen, and 35 per cent. in the latter. This enormous difference in proportions cannot be rejected on the ground that Harwood's drawing may be ' not exact ' (Bertin, 1934, p. 32). Harwood gave not only a figure, but also a description which agrees with the drawing.*

The difference in proportions in the two fishes compared cannot be explained by the difference in their size. The *smaller* Harwood specimen, 56 inches long, has a relatively *shorter* tail than Mitchill's specimen, 72 inches long. According to Bertin (1934, p. 18) with growth the preanal space becomes slightly *longer* and the tail shorter in Lyomeri (*Eurypharynx*). Such difference in proportions as is found between Harwood's and Mitchill's specimens is most probably connected with a different number of caudal vertebrae. It is well established that the number of

* **Harwood's data : total length 4 feet 6 inches. The ' sac ' of the body extends in length from the extremity of the snout about 20 inches ; ' at about one inch below the last point of its attachment with the body, the rectum was observed to perforate the sac '. Thus, the preanal length of the fish is about 19 inches, or just over 35 per cent. of the total length.**

vertebrae differs greatly in some *Saccopharynx*. Bertin (1934, p. 30) completely neglects this fact ; stating that all Saccopharyngidae have 250 vertebrae, he does not even mention that Girard (1895) found 138 vertebrae in his carefully studied specimen of *S. ampullaceus*. As already mentioned, in Johnson's specimen of *Saccopharynx* 140 vertebrae were found.

3. In Mitchill's specimen the anal fin begins 'just behind the vent' (Mitchill, p. 84), while in Harwood's *Saccopharynx* 'the anal fin commences at the posterior union of the [abdominal] sac with the body', which was found at about an inch from the anus (Harwood, pp. 54, 55).

4. The origin of the dorsal fin is closer to the head in Mitchill's specimen than in Harwood's. The predorsal space in the former is 78 per cent. the length of the body without the tail, and 95 per cent. in the latter.

There seems no reason to reject all these characters in the case of Mitchill's and Harwood's specimens and to consider *S. flagellum* as a synonym of *S. ampullaceus*, while creating new species on the strength of similar distinctions as Bertin did (1934, pp. 32, 33).

Besides the characters mentioned, Bertin (1934, p. 33) proposed some new ones. These are :—(1) The presence or absence of an abdominal prominence projecting beyond the anus, (2) presence or absence of a luminous caudal organ, (3) the difference in the number of dorsal fin rays in front of the vertical line of the vent (the latter character is another way of determining the position of origin of the dorsal fin used by earlier authors).

5. The difference in the size of the eye. (This character is used for discriminating *S. harrisoni* only, and is not discussed here.)

By using these characters Bertin (1934, 1938) has completely changed the arrangement of Saccopharyngidae ; obliterated one of the two known species (*S. flagellum*) ; and created three new ones (*S. johnsoni*, *S. schmidti* and *S. hjorti*). Thus these characters are worth considering in some detail.

(1) The presence or absence of an abdominal prominence and its size and shape depend upon the size of the prey swallowed by *Saccopharynx*, and the time which elapsed since it was swallowed, and then digested or rejected through the mouth of the aggressor. Such, or even larger, prominences are known in some fishes. When a *Chiasmodon niger* swallows a fish of bigger size than its own, its belly forms a monstrous sac, the anus and a large part of the anal fin are displaced, so that the fore part of the anal fin becomes turned down and backwards at an acute angle to the rest of the fin. When the food is digested the sac disappears gradually, the anus and the anal fin recover their original position. A series of *Chiasmodon niger* in the British Museum shows this clearly, and Hjort (Murray and Hjort, 1912, figs. 514–515) gives two stages of this process.

Similar things are known to happen with *Saccopharynx*. Harwood (1827, p. 53), describing the abdominal 'sac' of his specimen, writes :—'at about one inch below the last point of its [of the 'sac's'] attachment to the body, the rectum was observed to perforate the sac'. Thus, in *Saccopharynx* (as in *Chiasmodon*) the anus itself can be displaced and found *below* the junction of the abdominal sac and the body.

Johnson (1862, p. 277) describes the distention of the stomach of his specimen as 'unnatural' and 'painful'. But even more precise is Günther's (1887, p. 257) direct observation. Describing Johnson's specimen (*i. e.*, the *same specimen* which Bertin, 1934, p. 45, characterizes as having 'abdomen proéminent et formant une saillie en arrière de l'anus'), Günther says that when the large fish swallowed by this specimen was extracted, *the abdominal integuments of Saccopharynx contracted and the bag did not extend beyond the vent.*

Another species which according to Bertin (1934, p. 33) has a constant abdominal prominence projecting beyond the anus is *S. harrisoni* Beebe. Only one specimen of

this species is known, and all that is known about it is Beebe's (1932, pp. 63–67, fig. 12) description and figure in which no such prominence is described or figured. As Bertin has not seen this specimen, his statement appears unfounded.

Bertin (pp. 36, 48) refers to the fact that he found that Jesperson's specimen of *Saccopharynx* (*S. flagellum*) has an extended but 'empty' belly (filled with air ? or water ?). It seems likely that the fish had rejected the contents of its stomach just before it was fixed alive in formalin, and that this fixation prevented the tissues of the extended belly from retaking their normal proportions.

Harwood's idea that the 'abdominal sac' of the bathypelagic *Saccopharynx* is an 'air vessel', which is comparable to the air bladder of fishes or to the air sacs of birds, can hardly be maintained, though Bertin (1934, p. 36) seems to follow it.

By using Bertin's character of an abdominal sac projecting or not projecting beyond the anus, one risks describing as different species the same specimen before and after taking food.

(2) *The presence or absence of a caudal organ.*—The small organ found on the tip of the tail of Lyomeri is considered by some writers as a light organ, but others deny its photogenic properties. Brauer (1906, p. 135) writes cautiously that from its *external view* it seems possible that the organ may be a luminous one. Hjort (Murray, and Hort, 1919, p. 667), who observed a number of live Lyomari (mostly *Eurypharynx pelicanoides*), holds as quite certain that the caudal organ is not photogenic; Zugmayer (1911, p. 92) thus summarizes his histological study of this organ in Eurypharynx: 'rien ne permet d'admettre qu'il s'agisse là d'un organ photodique'; Nussbaum-Hilarowicz (1923, p. 60, pl. viii, figs. 12, 13) found no luminous tissue in this organ (in *Eurypharynx*) and quotes Zugmayer's conclusion. However, Beebe (1932, pp. 63–66) found that the caudal organ of *Saccopharynx harrisoni* was luminous when he observed the fish at the moment of its death in a dark room. The latter species has also larger and apparently better developed eyes than any other Lyomeri.

Whatever the function of the caudal organ may be, the peculiarities of its structure, or its presence or absence can be used for the purpose of systematics. Bertin recognizes seven species of Lyomeri (two *Eurypharynx* and five *Saccopharynx*) and only two of them (*S. ampullaceus* and *S. johnsoni*), according to Bertin, are deprived of the caudal organ. Bertin (1934, pp. 33, 35) had in hand a single specimen of '*S. ampullaceus*' (this specimen is considered here as a *S. flagellum*); he examined this specimen twenty years after its capture, and found no caudal organ; but Jesperson (1916, p. 147), who saw the same specimen alive, is much less definite on this subject and suggests that its caudal organ had possibly been lost.

Bertin has seen no specimens of his new species *S. johnsoni* (not recognized in this paper), which he characterizes by the absence of the caudal organ. However, Zugmayer (1911, p. 92) examined the specimen which Bertin holds as the type of his *S. johnsoni*, and described its caudal organ. It appears therefore probable that the caudal organ is found in all Lyomeri.

(3) From Bertin's key and description (p. 33 and following), *S. ampullaceus*, *S. johnsoni* and *S. harrisoni* have from 10 to 20 rays in front of the vertical line of the anus, while in his *S. schmidti* the anal orifice is under the 36th dorsal ray. This statement disagrees with the figures illustrating Bertin's own paper. The fish which Bertin calls *S. ampullaceus* (fig. 27) has the anal orifice under the 34th ray. According to Bertin, this figure is made after Jesperson's 'excellent figure'. However, in Jesperson's original figure of the same specimen (1916, pl.ii) the anal orifice is under the 45th dorsal ray. Bertin gives two figures of *S. schmidti* (pls. i and ii); one made by P. H. Winter from the fresh specimen, under the supervision of A. F. Bruun and P. Jesperson; and the other, made from the same specimen twenty years later by

F. Angel, ' qui joint à une grande adresse manuelle un talent d'observation de tout premier ordre '. On the first figure the anal orifice is under the 42nd dorsal ray, and on the second under about the 31st or 32nd.

Thus, in the figures illustrating Bertin's paper there is no such difference in the number of dorsal rays in front of the anus as he describes, and uses in his keys. Very curious in this respect is also Bertin's figure 41 of his new species '*S. johnsoni*'. This figure is described as made after Günther's figure (1887, pl. lxvi) of *S. ampullaceus*. However, according to Günther's figure *the first visible dorsal ray is about an inch behind the anal orifice and at the vertical line of the first anal ray*; from Günther's description (pp. 259, 260) the dorsal fin ' commences in front of the vent, but its anterior rays become visible only by dissection and with the aid of a magnifying glass '. Günther does not mention where the anal fin begins. Copying Günther's figure, *Bertin added* 13 *dorsal rays in front of the anal orifice, and showed the first anal ray just behind the anus.* Both characters are not found in the ' type ' of his species.

This brief revision shows how few characters can be used for discriminating the species of *Saccopharynx* in the present poor state of knowledge of this group.

2. *The Species of the Genus* Saccopharynx.

The material studied (two specimens only) is inadequate for a proper arrangement of this group, and the arrangement proposed here must be considered as a preliminary one.

Saccopharynx ampullaceus Harwood.

Ophiognathus ampullaceus Harwood, 1827.
Saccopharynx ampullaceus Cuvier, 1829; Johnson, 1862; Gill and Ryder, 1884; Günther 1887 (part); Goode and Bean, 1895; Girard, 1895 (part); Jordan and Evermann, 1896 (part); Regan, 1912 *a* (part); Jesperson, 1916 (part); Bertin, 1934, 1938 (part); Nobre, 1935.
Saccopharynx flagellum Günther, 1870 (part).
Saccopharynx johnsoni Bertin, 1934, 1938.

Brief characteristics of the species.—A few dorsal filaments (apparently no more than four) in the posterior part of the tail present; no dorso-lateral filaments along the sides of the dorsal ridge. A small caudal organ, flatter than that of *Eurypharynx* (Zugmayer, 1911, p. 92), present. The length of the body (from the tip of the snout to the vent) 27–36 per cent. of the total length; less than 150 vertebrae.

Type.—Harwood's specimen (No. 2)* was the first specimen of this species described and figured, but has not been preserved; Johnson's specimen (No. 3), preserved in the British Museum, which Johnson determined as *S. ampullaceus* and emphasized as identical with Harwood's specimen, could perhaps be considered as the neotype of this species (Schenk and McMasters, 1936, p. 8), but the state of preservation of this specimen is poor. However, some of the characters described and figured by Harwood can be recognized in it.

Type locality.—Both specimens were found in the North Atlantic and both floating on the surface (though they are bathypelagic fishes); Harwood's specimen was found 62° N., 57° W.; Johnson's about 33° N., 17° W.

Other specimens of this species are :—(No. 4), preserved in the British Museum, and possibly (No. 6) described by Girard, and not preserved. Girard does not mention or figure the dorsal posterior filaments and the caudal organ. As the specimen is lost, it is impossible to make sure whether these characters were overlooked by Girard or absent in his specimen.

* The numbers following the specimen refer to the table on pp. 290, 291, where more particulars of the specimens of *Saccopharynx* are given.

Johnson's specimen (No. 3), considered here as *S. ampullaceus*, was chosen by Bertin (1934) as the type of his new species *S. johnsoni* (not recognized here). Describing his *S. johnsoni*, Bertin attributed to it characters not found in the specimen: the absence of dorsal posterior filaments (present in the specimen); the absence of a caudal organ (described in this specimen by Zugmayer, 1911, p. 92); an anal fin beginning immediately behind the anus (in the specimen it begins at a distance of 8 mm. from the anus); ten (key, p. 33), or thirteen (fig. 41) visible rays in front of the vertical of the anus (no such rays could be found in the specimen, and according to Günther, no dorsal rays in front of the vertical line of the vent were visible without dissection when he examined this specimen undamaged). Finally, Bertin gives the relative length of the lower jaw of this specimen as 29·4 per cent. (p. 34) and 29 per cent. (p. 46) of the preanal length. Both figures are incorrect; they disagree with Johnson's measurements and with the dimensions of the specimen. The length of the jaw is 55 mm. ($2\frac{1}{5}$ inches) or 25 per cent. of the preanal length (from the tip of the snout to the anus).

Saccopharynx flagellum Cuvier

Saccopharynx (= *Stylophorus*), no specific name, Mitchill, 1824.
Saccopharynx flagellum Cuvier, 1829; Johnson, 1862; Gunther, 1870 (part); Gill, 1872; Gill and Ryder, 1884; Goode and Bean, 1895.
Saccopharynx ampullaceus Günther, 1887 (part); Girard, 1895 (part); Jordan and Evermann, 1896 (part); Regan, 1912 *a* (part); Jesperson, 1916 (part); Bertin, 1934, 1938 (part).

Brief characteristics of the species.—No dorsal filaments in the posterior part of the tail; numerous (30–50 on each side) dorso-lateral filaments along the sides of the dorsal ridge, from the head to the hind part of the tail, present; length of the body (from the tip of the snout to the anus) 19–22 per cent. of the total length. It seems probable that Bertin's (1934, p. 30; 1938, p. 14) statements on the number of vertebrae (about 250) found in *S. ampullaceus* must be referred to *S. flagellum*.

The caudal organ has not been described in this species, but according to Jesperson (1916) the specimen which he examined immediately after its capture had possibly possessed one.

Type.—Mitchill's specimen (No. 1), which Cuvier named *S. flagellum*, was not preserved.

The best known specimen of this species is that described by Jesperson (1916) as *S. ampullaceus* (No. 8).

Type locality.—North Atlantic. Mitchill's specimen was found floating off the surface at 52° N., 30° W. Jesperson's specimen was caught at 52° 22′ N., 24° 56′ W., at a depth between 2–3,000 metres.

Specimens.—Beside the two specimens mentioned, the specimen collected by the 'Albatross' (No. 5) belongs apparently to this species; it has not been described, but Goode and Bean (1895) figured it. Possibly, some of the 'incertae sedes' of Bertin (1934, p. 51) collected by the 'Dana' (Nos. 9, 10, 11), and the undescribed specimen of *Saccopharynx* which Bertin (1938, p. 14) mentions in his later account belong also to this species.

Saccopharynx harrisoni Beebe.

***Saccopharynx harrisoni* Beebe, 1932; Bertin, 1934; 1938.**

Brief characteristics.—No dorsal filaments in the posterior part of the tail; no numerous dorso-lateral filaments along the dorsal ridge; a complicated large caudal organ present, which is apparently essentially different from that found in other species of *Saccopharynx*. The eye is also apparently larger than in other species of this genus.

Type locality.—North Atlantic near the Bermuda Islands, at about 32° N., 64° W.

A single specimen is known (No. 13).

SACCOPHARYNX SCHMIDTI Bertin.

Saccopharynx schmidti Bertin, 1934, 1938.

A doubtful species having a few dorsal filaments in the posterior part of the tail, no dorso-lateral filaments, a small caudal organ (all characters found in *S. ampullaceus*), but having a relatively longer tail and shorter body (22 per cent. in total length, as in *S. flagellum*). The number of vertebrae is unknown.

A single specimen (No. 12) collected in the South Pacific at 33° 39′ S., 159° 00′ E.

No judgement can be given here about the fish which Bertin (1938, p. 13) calls *Saccopharynx hjorti*. Bertin had not seen this fish, and all that is known about it is the little sketch published in the general description of the voyage of the 'Michael Sars' (Murray and Hjort, 1912). Hjort mentions that the figure represents a new genus of Gastrostomidae. He obviously intended to give the description, and to name his fish when the general account on fishes collected by the 'Michael Sars' is published. Lea (1914, p. 43), describing the larvae collected by the 'Michael Sars', tactfully refers to this fish as an 'undescribed form which for convenience we may call species A'. He mentions that the fish has an organ attached to the tip of its tail 'but totally different in structure' from that of *Gastrostomus* (=*Eurypharynx*), and that its foremost dorsal ray is situated much farther back than the foremost anal ray. Describing this fish as his new species from the characters given by Lea, Bertin gives no type locality, no depth at which the fish has been taken and no size of the specimen he describes. However, all these data are given by Murray and Hjort (1910, 1912). (See the table on pp. 290, 291, of this paper.)

It would seem premature to discuss the systematic position of fish which has not yet been described, and one may hope that Prof. J. Hjort will give a description of his interesting specimen now that difficult times seem to be over.

3. *The Four Specimens of* Eurypharynx.

Determination of Eurypharynx pelicanoides *Vaillant.*—The *Eurypharynx* are much more common than the *Saccopharynx*. Bertin (1934, p. 25) lists 125 known specimens of *Eurypharynx*. This list does not include eighteen specimens (one young) collected by 'Michael Sars' in 1910 (Murray and Hjort, 1912), and the two specimens taken by the 'Discovery', described by Norman (1930, p. 337). Thus, no fewer than 142 specimens of *Eurypharynx* have been examined by scientists, and this has helped to clarify the confusion brought into the systematics of this group by Vaillant's (1882) careless, inaccurate, and misleading descriptions and figures (Bertin, 1934, p. 9). It is now certain that a single genus of Eurypharyngidae is known so far, with apparently a single species—*Eurypharynx pelicanoides* Vaillant.

This species can be thus characterized: Body (from the tip of the snout to the anus) three times, or slightly less, in total length (length of body against total length 28–33 per cent.); the body relatively longer in larger specimens. Length of the lower jaw about two-thirds, or slightly more, of the length of the body (three specimens only measured). First dorsal ray in front of the branchial orifice; first anal ray close to, but not immediately behind, the anus. The caudal organ is small and consists of two black oblong folds crowned on each side by 6–11 small rounded 'papillae'. It is situated on the dorsal side of the posterior part of the tail and roofs the space from the tip of the tail covering the urostile and about 6 posterior vertebrae (*fide* Bertin, 1934, fig. 7).

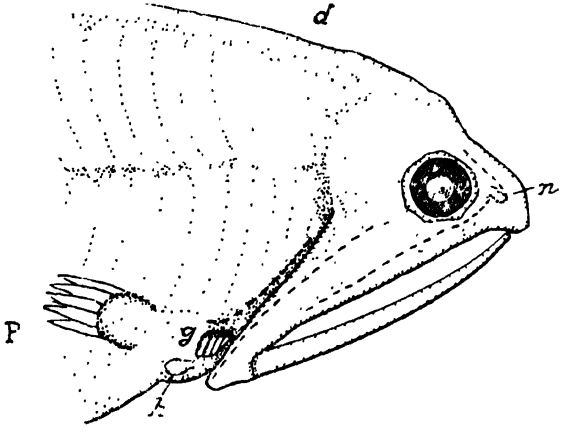
According to Bertin (1934, p. 9) the *Gastrostomus pacificus* described by Bean (1904) does not differ from *Eurypharynx pelicanoides*, and the *Macropharynx longicaudatus* of Brauer (1902) is also an *E. pelicanoides*.

It would be difficult to maintain the validity of the *E. richardi* described from a single specimen by Roule (1914). This specimen had the lateral line under-developed on one side of the body, and Roule not without well-justified hesitation, considered this feature as of taxonomic importance (for details see Bertin, 1934, p. 24). Fowler (1925 *a*, p. 2 ; 1925 *b*, p. 75) considers *E. richardi* as the type of a new subgenus.

The Three Adult Specimens of Eurypharynx pelicanoides.

Specimen No. 1930.1.12.887 ' Discovery ' Expedition, 12. viii. 27 ; Station 281 ; 00° 46′ 00″ S., 5° 49′ 15″ E. ; depth of the net 850–950 (–0) m. Total length 295, length of the body 86, length of the lower jaw 58 mm. In good condition except for the skin being broken in several places.

Specimen (not registered).— ' Discovery ' Expedition, 19. vii. 1927 ; Station 287 ; 2° 49′ 30″ S., 9° 25′ 30″ W ; depth of the net 800–1,000 (–0) m. Total length 170, length of the lower jaw 36 mm. The specimen was found in poor condition. It was then clarified and stained with alizarin. The description of the skeleton of *Eurypharynx* given below is made from this specimen.



TEXT-FIG. 1.—Anterior part of the body of a larva of *Eurypharynx* (?).
Right side. ×10. Diagrammatic.

d., dorsal fold ; *g.*, gill aperture ; *h.*, heart seen through the transparent tissues ; *n.*, nostril ; *p.*, pectoral fin. The series of the lateral line system shown by dotted lines.

Specimen No. 1934.12.19.14.— ' Princesse Alice ', 29. vii. 1914 ; Station 3608 ; 30° 35′ N., 22° 57′ 30″ W. ; depth of the net 0–2,600 m. Total length 272, length of the body 77, length of the lower jaw 54 mm. The condition of the specimen is satisfactory, though the skin is broken in several places.

Larva of Eurypharynx sp. (text-fig. 1).

Specimen (not registered).— ' Discovery ' Investigation Station 281, 00° 46′ 00″ S., 5° 40′ 15″ E., 12. viii. 27, depth of the net 850–950 (–0) m. This specimen is in the so-called ' semilarval ' stage.

The tip of the tail is missing, which makes the measurement of the total length uncertain. Otherwise the specimen is in good condition.

Dimensions.—Length 29 mm. Compared with figures of the only semilarva of Lyomeri ever described and figured (Murray and Hjort, 1912, fig. 545 *b* ; Lea, 1914, pl. vi, fig. 5) the missing part of the tail seems about 4 mm. long. Thus the total length of the specimen is about 33 mm.

The fish is compressed from side to side, and deep; the breadth of its body behind the pectorals is less than one mm. while its greatest depth, in front of the vent, is 7·5 mm. The body narrows posteriorly, and at the place where the tail is broken off it is about half a mm. deep. The axis of the cranium is inclined anteriorly downwards at about 45° to the main axis of the body. The suspensorium is long, its distal end being directed down and backwards. The gape of the mouth is large, its upper edge is cutaneous, extending from the rostrum to the posterior quarter of the suspensorium, where the latter forms the posterior part of the edge of the mouth gape. No other skeletal elements along the upper edge of the mouth gape could be detected (the specimen was not dissected and not clarified). The eye is about as large as the snout, it projects laterally beyond the orbit and is covered with transparent skin. The posterior (dorsal) edge of the suspensorium is intimately united by integuments with the body, the external branchial aperture is small, about half the diameter of the eye; it is situated at a short distance behind the distal part of the suspensorium, and in front of the pectoral fin. The space between the base of the pectoral and the hind edge of the branchial aperture is slightly more than the diameter of the eye. The cutaneous membrane above the gill opening is not supported by bones and short; it does not cover the gills. Four gills are visible through the opening. The posterior part of the cranium is covered by strong muscles, and it is not possible to estimate the length of the cranium without removing these muscles. The ethmoido-rostral part is strongly curved downwards at about the level of the nostril (*n*); the latter (one only visible on each side) is in front of the eye. The cranium is compressed from side to side, its greatest breadth behind the eyes is about 2 mm.; the breadth of the inter-orbital space about half the diameter of the eye. The mandible is 5 mm. long, its rami are slender, their tips upturned and reaching the rostrum from below. The posterior ends of the mandible are covered by a fold of skin extending downward from the suspensorium. Nussbaum-Hilarowicz (1923, p. 57) described a similar fold in the adult *Eurypharynx*. The tips of the rami of the mandible articulate with each other movably, but not loosely. There are no teeth. There is no 'tongue', *i. e.*, no hyoid bars, basi-hyals, or branchial elements extend into the oral cavity.

Fins.—The pectoral fins are lobate, their lobes are flat, rounded discs slightly smaller than the diameter of the eye, they unite with the body at its 7th segment, two segments behind the branchial orifice. The fin rays are transparent and broad, of uniform structure; five in number.

A thick semi-transparent dorsal fold (*d*) extends along the head and along the body from the eye to the posterior end of the body. This fold is the deepest at some distance behind the vertical line of the vent. From the 20th segment backwards, small rays of the dorsal fin crown this fold. I counted 168 dorsal rays, but owing to the small size of the rays, counts are difficult and may not be exact. The rays correspond to about 72 segments of the body, two or three rays corresponding to one segment. A similar fold extends along the ventral side from the posterior end to the vent; all along its lower edge rays, similar to those of the dorsal fin, are found; the first ray being under the 34th segment (one segment behind the anus). The number of the anal rays is 135, corresponding to about 60 segments.

Number of Segments.—The first one or two segments and a few last ones are indistinct; the tip of tail with about six or eight segments is missing. Thus no exact number of segments can be given. I counted 32 (possibly there are 33) segments in front of the vent and 60 behind the vent, 92 or 93 altogether. Thus the total number of segments including those of the lost part of the tail is probably about 100, possibly slightly more, but certainly not 140.

The lateral line system appears as whitish (unpigmented) oblong spots arranged in series or lines (on fig. 1 it is shown by dotted black lines). There are no papillae projecting from the skin. The series of this system are:—(1) The supraorbital

series, from above the nostril, along the head above the orbit ; it becomes indistinct in the region of the orbit, and could not be followed further. (2) The infraorbital series originates from under the nostril and extends along the upper edge of the gape of the mouth to about three-quarters the length of this gape. (3) A series along the suspensorium of which the significance is not clear (see p. 323,' Quadrato-jugal series ? '). It originates near the hind edge of the orbit (its anterior part is indistinct) and extends along the suspensorium to the mandibulo-quadrate articulation. No sign of lateral line was found on the mandible. (4) Another series, of which the significance is also uncertain, originates behind the eye, extends backwards and downwards along the side of the body to the branchial aperture, and proceeds backwards along the branchial fold to the pectoral fin ; the main course of this series is parallel to the suspensorium, and it runs just behind and dorsally to the suspensorium. (5) The main lateral line of the body is distinguishable only from the 6th or 7th segment, it extends backwards nearly straight along the midline of the side of the body. I could find no curve of the lateral line described and figured by Lea (1914, p. 44, pl. vi, fig. 5).

The structure of the lateral line system in adult Lyomeri is described on p. 321.

The heart (*h*) is visible through the transparent tissues ; it lies between the bases of the pectoral fins and the branchial apertures. The *aorta branchialis* follows its normal course from the heart towards the gills (not towards the anus and away from the gills ; compare Bertin, 1938, fig. 14.)

Pigmentation.— All the body and the head are covered with small dots of dark pigment. The pigmentation is much thicker along the upper edges of the gape of the mouth, behind the suspensorium, and at the bases of the dorsal and anal fin rays. A dark, heavily pigmented, spot is found on the ventral surface in front of the vent.

Proportions.— (FIRST COLUMN shows the number of times contained in the total length ; SECOND COLUMN, in percentages of the total length).

The greatest depth of the body	4·4	23
The greatest breadth of the head (behind the orbits) ..	16·5	6
The length from the tip of the snout to the gill opening ..	7·3	13
The length from the tip of the snout to the vent	2·2	45
The length from the tip of the snout to the first dorsal ray	3·0	33
The length of the lower jaw	6·7	15

Hjort (Murray and Hjort, 1912, p. 749, fig. 545) discovered that the Lyomeri pass in their development through a leptocephalus stage. Lea (1914, pp. 43–46 pl. vi, fig. 5) described the semilarva found by Hjort under the name of *Leptocephalus Gastrostomi Bairdi* (*Gastrostomus bairdi=Eurypharynx pelicanoides*), and suggested that the *Leptocephalus latissimus* described by Schmidt (1909, p. 4 ; 1912, footnote on p. 45) is a larva of another form of Lyomeri.

Roule (1934, pp. 142, 143) described and figured a fish-like animal collected by the ' Dana ' Expedition, which he calls a ' Sémilarve en métamorphose d'un Apode Lyomère '. Roule has apparently not seen the descriptions of Hjort (Murray and Hjort, 1912) and Lea (1914) of semilarvae of Lyomeri (see below, p. 339, ' Monognathidae ').

Bertin (1938) had in hand the unique series of larvae of Lyomeri collected by the ' Dana ' Expedition, consisting of 123 specimens. According to Bertin, all these larvae belong to species of the rare *Saccopharynx* and none to the much more common *Eurypharynx*. Thus from Bertin's determination the ' Dana ' collection contains 59 specimens of *Eurypharynx* in post-larval stage, but contains not a single larva of this genus ; while the genus *Saccopharynx* is represented in the same collection by 123 larvae, and by only five specimens in the post-larval stage.

Bertin calls all these 123 larvae *Leptocephalus pseudolatissimus*. He does not compare his *L. pseudolatissimus* with the larva of *Eurypharynx* (*L. Gastrostomi bairdi*) described by Hjort and by Lea.

Bertin's attribution of all the larvae collected by the 'Dana' to *Saccopharynx* does not seem convincing. From his description, the '*L. pseudolatissimus*' has from 115 to 124 segments, but from his very clear figure 3 (pl. ii) the 18 mm. long specimen (st. 1322.ii) has only 100 segments. The smallest number of vertebrae found in *Saccopharynx* is 138 not including some indistinct vertebrae at the posterior end of the tail. The number of vertebrae in *Eurypharynx* is much smaller (106–110). Thus by its *main feature* (the number of segments in the larva compared with the number of vertebrae in adult specimens, Schmidt, 1912, p. 40) the *L. pseudolatissimus* is more likely to represent the larva of *Eurypharynx* than of *Saccopharynx*; or possibly these 123 larvae contain specimens belonging to both these genera, on the larvae of some other fishes also.

It is not certain to which genus the larva of the 'Discovery' collection belongs. From the small number of segments, and from the number of rays in the unpaired fins, it is likely to be the *L. gastrostomi bairdi* Lea, *i. e.*, the larva of *Eurypharynx*, but it differs from the latter by the absence of the anterior curvation of the lateral line, by the strongly bent ethmoid part of the head, by the different position of the branchial aperture in relation to the base of the pectoral fin, and by the number of pectoral rays. It is difficult to judge how real these distinctions are without an immediate comparison of the specimens. As the course of development of Lyomeri is not known, the taxonomic value of these characters is not clear. Therefore the specimen of the 'Discovery' is described here as a young *Eurypharynx* with a query.

II.—Notes on the Skeleton of Lyomeri.

1. *On the General Structure of Lyomeri (with a description of the gill apparatus of* Eurypharynx).

The material in hand for the present study is inadequate. It consists of one badly damaged and dissected specimen of *Sdccopharynx ampullaceus* (Johnson's specimen, described in this paper, p. 288) and one small defective specimen of *Eurypharynx pelicanoides* ('Discovery' 1927, station 287, see p. 299), which earlier had been clarified and stained with alizarin. However, as little is known about the osteology of Lyomeri, even this poor material is worth describing.

The structure of Lyomeri is mainly known from the study of *Eurypharynx* by Gill and Ryder (1883), Zugmayer (1911, 1913) and especially Nussbaum-Hilarowicz (1923); but very little indeed is known about the anatomy of *Saccopharynx*. The lack of knowledge on the structure of these fishes is well illustrated by Bertin's (1934) monograph on Lyomeri. Even the skeleton, which usually attracts the attention of ichthyologists, is hardly known at all. For instance, it is not known whether there is an ossified lower jaw or not. Regan (1912 *a*, p. 348) characterizes Lyomeri as having three bones in the lower jaw (dentary, articular and angular), while Bertin (1932 *b*, p. 147; 1934, p. 4) holds the complete absence of all bones of the lower jaw as one of the main features of this order. It is not known whether the Lyomeri have a supraoccipital or not (compare Zugmayer, 1911, 1913; Regan, 1912 *a*; and Nussbaum-Hilarowicz, 1923, p. 55). The same uncertainty exists about the vomer and parasphenoid (compare Gill and Ryder, 1883, pp. 266; Nussbaum-Hilarowicz, 1923, p. 58). All that is known about the skeleton of the pectoral fins and girdle of Lyomeri, is Bertin's (1934, p. 20) statement, according to which the shoulder girdle is 'réduite à quelques pièces cartilagineuses,' a statement which is neither precise nor correct. The most remarkable and unique feature of *Eurypharynx*, the presence of *six* well-developed and functional visceral clefts, has not attracted

much attention from ichthyologists ; and the hyoid and branchial elements of its skeleton have not been investigated carefully. These are only a few examples. No wonder there is no unanimity among ichthyologists about the relations and origin of these fishes !

The names of skeletal elements used by some writers on Lyomeri are unusual and it is not always clear what elements they describe. It requires more time and effort to disentangle the puzzle of wrong nomenclature than the actual study of the fish. Zugmayer (1913, fig. on p. 5) terms the anterior part of the basioccipital ' sphénoide,' which, according to his explanation (p. 1), is equivalent to the parasphenoid. Nussbaum-Hilarowicz (1923, pl. viii, fig. 1) calls the pterotic ' prootic ', a name never used before for this bone. Bertin (1934, fig. 11, pp. 19, 39) repeats both these mistakes. Zugmayer and Nussbaum-Hilarowicz refer to the rostral end of the ethmoid cartilage as ' nasale ', a name not used for this cartilage ; Bertin (1934, pp. 18, 30, 39) refers to the same element as ' nasal ' and ' l'os nasal ', the latter being incorrect and misleading. The same writer (1934, p. 4) considers the absence of opisthotics and of the basisphenoids as the most important characteristics of all Lyomeri, but on p. 18 he describes both these bones in *Eurypharynx* and shows them on figs. 10 and 11 ; on p. 39 he describes the opisthotics in *Saccopharynx*, and shows them in fig. 34. These are a few instances to show how far the practice of inaccurate use of the skeletal nomenclature has gone, and how the wrongly used names make it impossible even for the writer himself to understand what he means.

The study of the skeleton of Lyomeri is also made more difficult by the regrettable practice of some ichthyologists of describing not the elements which they really find in an unusual fish, but the elements which, according to their preconceived idea, must be found there. Thus, nearly all skeletal elements absent in Lyomeri have been described as present. Such, for instance, are :—the supraoccipital, the radii branchiostegi, the premaxillary, the orbital series, and several others. Describing the elements which the writer has not found, he usually qualifies them as ' rudimentary ', ' vestigial ', ' very small ', remarks that they are ' tout à fait rudimentaires et il n'est pas possible de les distinguer avec certitude ' but still describes them as present and even shows them in figures. This makes the matter more obscure for future investigators.

The homology of skeletal elements of fishes is not an easy problem. In Lyomeri, whose development has not been studied, and whose skeleton (in adult state) is only superficially known, it is even more difficult. Thus, to avoid misunderstanding the skeleton of the Lyomeri is described here in some detail, and the supposed homology of its parts discussed. The names used by other writers for the same elements are also referred to.

I would like, however, to stress that the present study is but a preliminary one, that the homologies of elements proposed here are in many instances only guesses, and that the osteology of this group needs a complete revision, based on good and plentiful material.

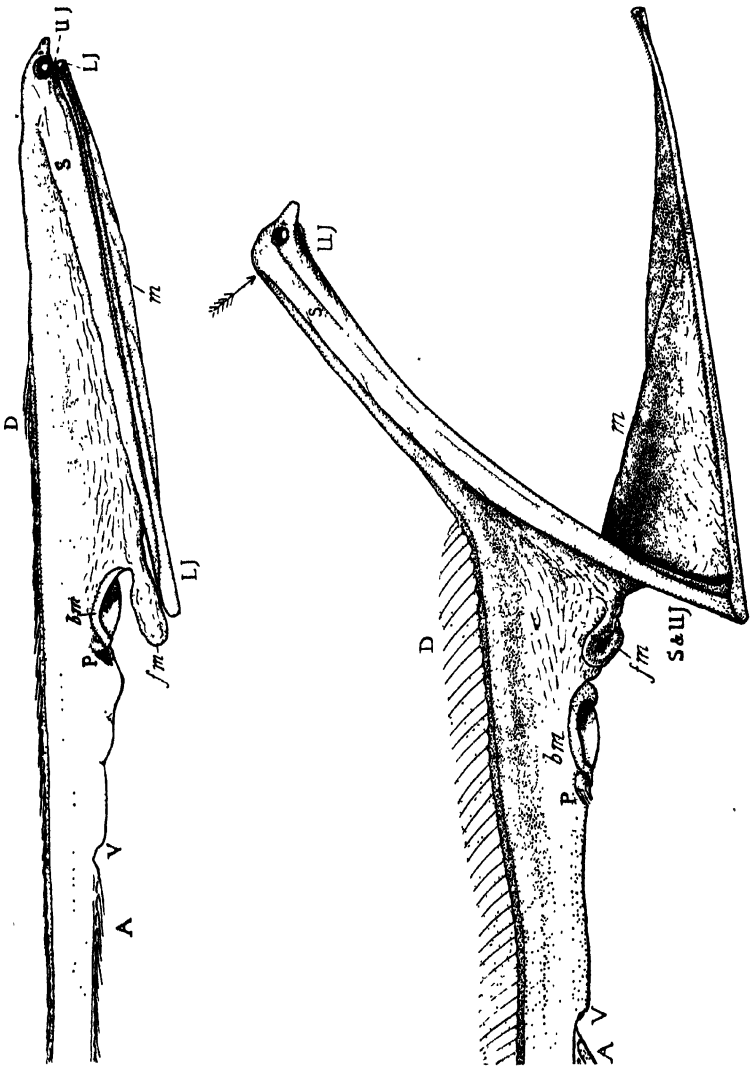
The structure of Lyomeri differs substantially from other fishes, and it seems necessary to outline first some general peculiarities of this group (text-figs. 2–5).

1. The head of Lyomeri consists of two widely separated parts : (*a*) the neurocranium with the suspensorium and the jaws joined to it, and (*b*) the branchial apparatus set at a considerable distance behind the cranium, and not connected with the latter, nor with the jaws, by bones, differentiated muscles or ligaments.

2. The shoulder girdle is situated under the 15th (*Saccopharynx*) or 19th (*Eurypharynx*) vertebra ; the branchial apparatus under the 12th–14th vertebrae in *Saccopharynx* and 16th to 18th in *Eurypharynx*. The heart lies far behind the

cranial part of the head, under the 15th to 17th vertebrae in *Saccopharynx*, and under the 17th to 18th vertebrae in *Eurypharynx*.

Thus 14-18 vertebrae situated between the neurocranium and the hind part of the branchial apparatus form a part of the head as much as of the body.



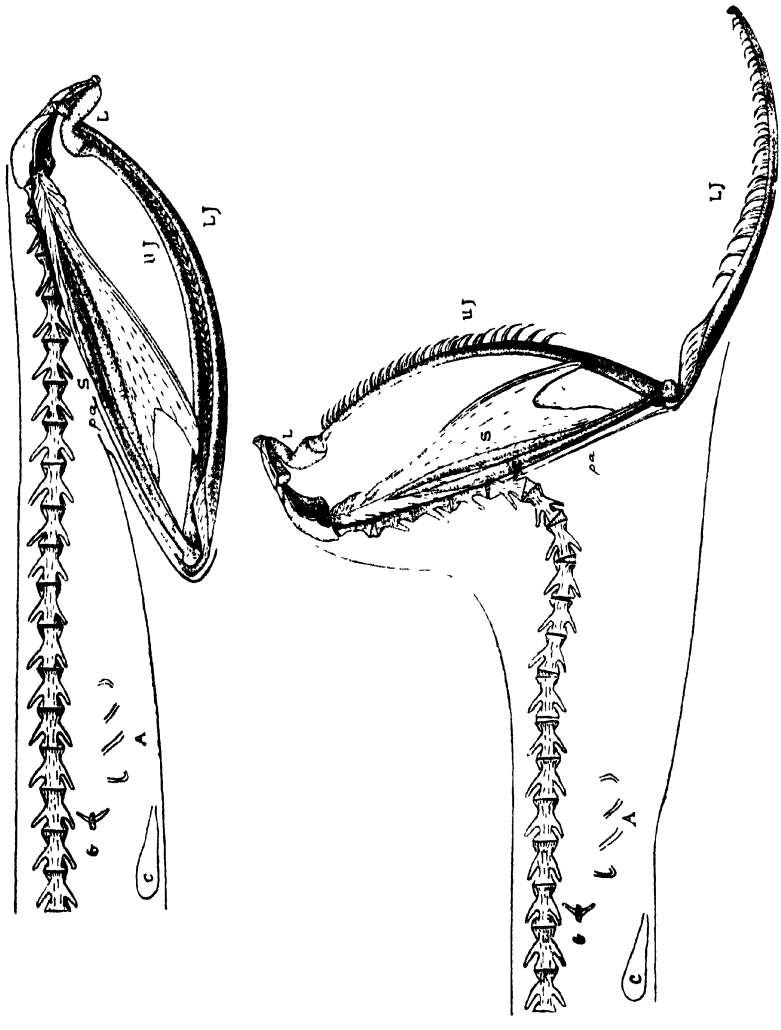
Text-figs. 2 & 3.—Diagrams of the anterior part of the body of *Eurypharynx pelicanoides*. **Text-fig. 2** mouth shut, the rami of the mandible put close together; **text-fig. 3** mouth slightly open, the rami of the mandible expanded laterally. Enlarged.

***bm.*,** fold of integuments covering partly the branchial clefts; ***fm.*,** folds of the pharyngo-oral sac; ***m.*,** the floor of the pharyngo-oral cavity; *A.*, anal fin; *D.*, dorsal fin; *LJ.*, lower jaw; *P.*, pectoral fin; *S.*, suspensorium of the lower jaw; *UJ.*, upper jaw; *V.*, vent. The arrow shows the posterior end of the neurocranium (basioccipital). Note the different shape of the head in these two figures; this is due to the movably joined parts of the neurocranium.

3. The elements suspending the lower jaw to the cranium are long and slanting down and backwards at an acute angle to the main axis of the body so that they are lying closely and almost parallel to the anterior vertebrae. There are no opercles or opercular folds connected with the suspensorium, and the latter is not separated

from the rest of the body by a slit leading into the branchial cavity. Thus the suspensorium is intimately united by integuments with the anterior vertebrae and the movements of both structures are co-ordinated.

When the distal end of the suspensorium moves forward and its position becomes at about a right angle to the main axis of the body, the four or five anterior vertebrae



TEXT-FIGS. 4 & 5.—Diagrams of the anterior part of the skeleton of *Saccopharynx ampullaceus*. Lateral view. Text-fig. 4 mouth shut, text-fig. 5 mouth open. *A.*, branchial arches; *C.*, heart; *G.*, pectoral girdle; *L.*, ligament attaching the upper jaw to the neurocranium; *L.J.*, lower jaw; *S.*, suspensorium of the mandible; *U.J.*, upper jaw; *pa.*, ossified tendon of the *m. abductor mandibulae*.

rise upwards and stand up also at a right angle to the main axis of the body. This is the position when the mouth and the throat of the fish can be wide open (text-figs. 2–5).

4. The complicated apparatus on the ventral side of the head found in most of the teleostomes, and consisting of the muscular 'isthmus', hyoid bars, basal elements

of the branchial and hyoid arches (' copula ' and ' tongue '), the branchiostegal rays, and all the muscles, ligaments and membranes connected with the elements, are either entirely missing or set far back, so that the ' floor of the mouth ' is formed by a single uninterrupted membrane of three layers : the outer skin, the epithelium of the inner surface of the mouth, and between them a third layer consisting of connective tissue, with separate muscular and elastic fibres disposed in different directions (Nussbaum-Hilarowicz, 1923, p. 25). Therefore the lower jaw is depressed in a way different from that usually found in fishes. In Lyomeri it is depressed by a special muscle (*extensor mandibulae*, Gill and Ryder, 1883) which originates at the edge of the hinder part of the pteroticum and is inserted into the posterior end of the lower jaw, behind the articulation of the latter with the quadrate.

The shoulder girdle, the heart, the ventral aorta and the ventral parts of the branchial arches do not move anterio - posteriorly (as they do usually in fishes) when the mouth opens or shuts again.

5. The branchial apparatus is somewhat different in *Eurypharynx* and *Saccopharynx* and the description given here is made from *Eurypharynx* (text-figs. 6, 7, Pl. **2**, fig. 1). As Agassiz (1888, p. 36) remarks, ' the respiratory apparatus [of *Eurypharynx*] is unique among bony fishes '. Six visceral clefts pierce the wall of the body into the gut. The first cleft is elongated more or less horizontally, its external aperture is compressed dorso-ventrally, while the five next are compressed from side to side and have a more or less vertical extension. The five integumentary spaces or partitions between the clefts are broad and fleshy, thus the clefts are tubular. The arches, *i. e.*, the skeletal elements supporting the septa between the clefts, have never been studied precisely. Nussbaum-Hilarowicz (1923, p. 66) describes the skeleton of an arch as consisting on each side of ' 3–4 small, elongated irregular cartilages embedded in the fibrous connective tissue '. These cartilages are not distinguishable without preparing sections and I had no material in hand for such a study. There are no gill-rakers. Nussbaum-Hilarowicz says that there are only four branchial arches in *Eurypharynx*, but Bertin (1934, p. 23), who had magnificent material in hand, states quite definitely that there are five branchial arches in this fish. Apparently none of these scientists investigated whether there are any skeletal elements behind the sixth cleft. According to Nussbaum-Hilarowicz (1923, pl. ix, fig. 13) each of the six internal apertures of the branchial clefts is surrounded by a muscular sphincter. Thus these muscles are situated medially to the branchial arches. *There are five holobranchs between the six gill clefts.* There is no hemibranch on the anterior wall of the first cleft and no hemibranch on the hind wall of the last cleft. No ventral hyoid elements are attached to the *suspensorium mandibulae*. There are no basal hyoid or basi-branchial elements, and the left and right halves of the visceral arches are separated from each other. A part of the belly (*V.*) or of the chest containing part of the liver and the heart, is situated ventrally to the branchial apparatus. A fold (*bm*) encircles the external branchial apertures of the left and right sides together with the part of the belly situated under the gill apparatus. Posteriorly these folds pass just in front of the pectoral fin. Their extension is shown in text-figs. 6 and 7. In Pl. **2**, fig. 1 (lateral view) the fold is cut off, and a double line shows where it separates from the body. The lateral parts of this fold are deep, and partly cover the visceral clefts and the gills, forming on each side a kind of imperfect gill chamber separated from its fellow ventrally by the projecting part of the belly (*V*). But the folds surrounding the branchial apparatus are too short to close these chambers ventrally. This suggests that the breathing process of *Eurypharynx* is different from that usually found in fishes.

6. The skeleton of Lyomeri differs markedly from that found usually in Osteichthyes and is described separately in *Eurypharynx* and *Saccopharynx*.

2. *The Skeleton of* Eurypharynx.

(a) *The skull.*—The general structure of the skull has the peculiarities which correspond to those mentioned in the description of the head. It can be added that the eyes are anterior in position, and that the olfactory organs are very small; the neurocranium in proportion to the length of the head and of the jaws is extremely small; about seven times as short as the suspensorium or as the lower jaw. The axis of the cranium is inclined downwards and forwards at about 45 degrees to the main axis of the body, when the head is in its ordinary position. But as the articulation of the skull with the first vertebra is a movable one, this angle can be changed.

The visceral skeleton.—The visceral skeleton of *Eurypharynx* is a puzzling structure. The suspensorium and the jaws are formed by three rod-like elements of about equal length, the upper jaw being always slightly shorter than the lower. The rod forming the suspensorium articulates with the ventral side of the cranium by a single rounded condyle. The articulating groove is large and deep, its medial wall is formed by the prootic and lies laterally and very close to the jugular canal or the canal for the passage of the hyomandibular branch of the facial nerve. The long body of the suspensorium extends backwards and slightly downwards to the vertical line of about the 18th vertebra, where it articulates with the mandible. The main rod of the suspensorium is partly cartilaginous, its shaft being only perichondrally ossified, and its proximal end is cartilaginous; examination under the microscope shows that this rod is subdivided into two parts: a proximal shorter part and a longer distal one. Thin bony lamellae extend along this rod and firmly unite both these parts.

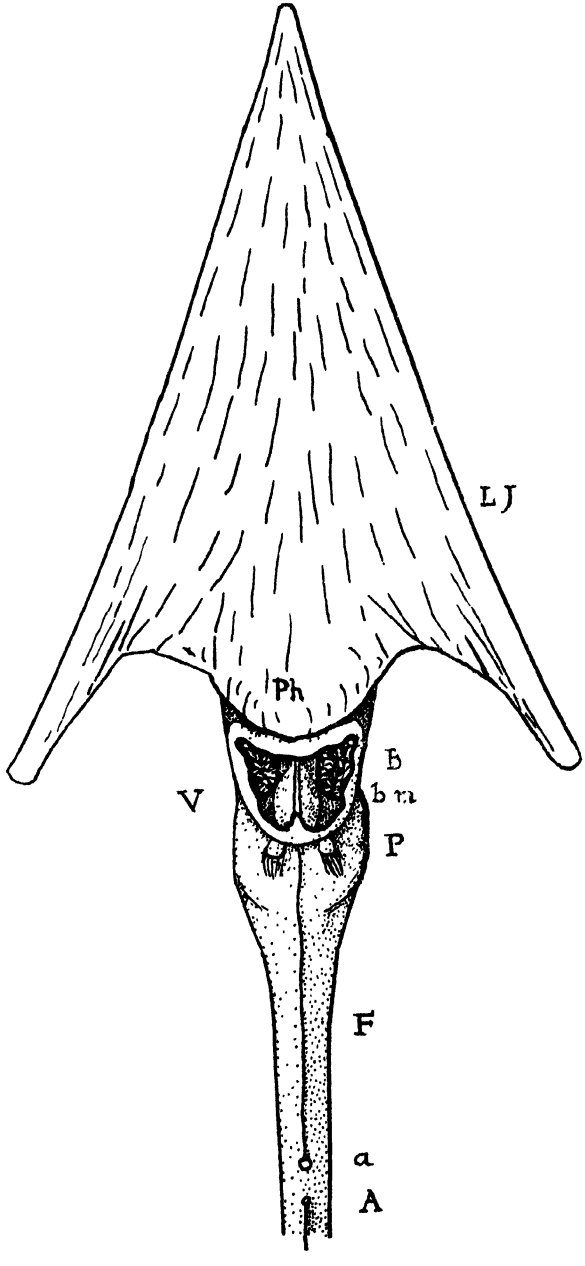
The tips of the rods forming the right and the left rami of the upper jaw articulate with each other on the ventral surface of the cranium (under the middle of the vomer) at the vertical line of the centre of the eye. At about one-third of its length the upper jaw comes close to the suspensorium and extends backwards along its ventral edge, and finally is attached by ligaments to the medial surface of the distal end of the quadrate, and to the inner (medial) surface of the mandible just in front of the mandibulo-quadrate articulation. The *m. adductor mandibulae* inserts into the lower jaw laterally to the upper jaw.

No elements corresponding to the ventral part of the hyoid arch are attached to the suspensorium, the latter has no process corresponding to the *processus opercularis* and there is no element corresponding to the symplectic.

A branch of the nerve which is supposed here to be the *n. facialis* perforates the lamella of the proximal limb of the suspensorium close to its articulation with the neurocranium. A considerable stretch of the wall of the body separates the suspensorium from the anterior visceral cleft which is situated caudally and ventrally to the proximal element of the suspensorium. In the septum situated behind the anterior cleft cartilaginous elements supporting this septum are found. Similar cartilages support the septa between the next four visceral clefts; it is not known whether any skeletal elements are found behind the sixth cleft.

One can see from this general description that the visceral elements of *Eurypharynx* differ fundamentally from those of Osteichthyes, and they are considered further in more detail.

The suspensorium.—The proximal element of the suspensorium corresponding in position and in relation to the facial nerve to the hyomandibular, articulates with the neurocranium by a ball-like condyle which enters into a deep groove on the ventral side of the cranium (Pl. 3, fig. 2). This articulating groove is described on p. 318. From a morphological examination the proximal epiphysis of this bone recalls the

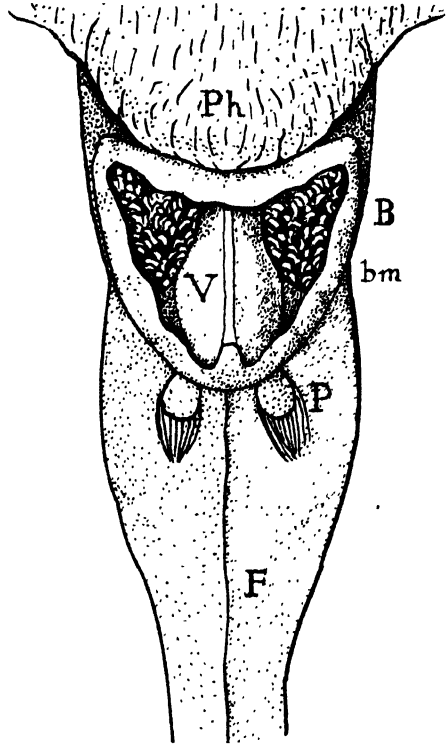


TEXT-FIG. 6.—Anterior part of the body *Eurypharynx pelicanoides*.
Ventral view. Diagrammatic. ×2.

a., vent; *bm.*, branchial fold; *A.*, anterior end of the anal fin; *B.*, branchial chamber with the gills; *F.*, ventral medial fold in front of the anus; *L.J.*, lower jaw; *P.*, pectoral fin; *Ph.*, pharyngeal fold; *V.*, anterior part of the belly.

cartilaginous epiphyses of bony fishes as described by Haines (1942, p. 268), its tip being of cartilage and entering into the shaft of the bone 'like a cork into the neck of a bottle', but the minute structure of this bone has not been studied.

The shaft of the hyomandibular is long, rounded in transverse section, and well ossified on the surface. The distal end of the hyomandibular is cartilaginous and has a flat facet for articulation with the similar upper facet of the distal element of the suspensorium, which is considered here as the quadrate. A thin well-ossified lamella arises close to the proximal end of the hyomandibular, and extends along the medial side of its shaft beyond the hyomandibular-quadrate articulation; distally it joins firmly to the medial side of the quadrate. This lamella is broader



TEXT-FIG. 7.—Branchial apparatus of *Eurypharynx pelicanoides*. Ventral view. Diagrammatic. ×4 (Enlarged detail of text-fig. 6.) Lettering as in text-fig. 6.

than the shaft of the hyomandibular and its upper end forms considerable anterior and posterior projections. The projections serve for muscular attachment. As described above, the posterior part of this lamella is perforated by a branch of the facial nerve. A very thin thread-like ossification stretches laterally over the hyomandibular-quadrate articulation, and along both parts of the main rods of the suspensorium. It can be distinguished on a clarified and stained skull. It probably corresponds to the much larger ossification (*x*) of *Saccopharynx* (p. 330, text-fig. 13).

The articulation of the suspensorium with the cranium.—This articulation is like ball and socket, and suggests a great mobility. Earlier writers described it as movable

not only laterally (in the horizontal plane), but also forwards and backwards (in the vertical plane). The specimen studied has lost most of its muscles, and I could not verify this. In any case, the skin over the back, uniting the suspensoriums of the left and right sides, is very tight, and would not allow any strong forward movements of the suspensorium. The upper jaw, attached to the distal end of the suspensorium and to the ventral surface of the cranium, would also hinder such movements. An attempt to move forwards the distal end of the suspensorium automatically affects the anterior vertebrae, which rise to a vertical position (text-figs. 2–3).

The articulation of the hyomandibular with the quadrate. - The hyomandibular articulates directly with the quadrate. There is no symplectic. The flat facet of the cartilaginous end of the hyomandibular fits exactly to the similar upper facet of the quadrate. This articulation seems to be immobile. As already described, a strong and well-ossified lamella of the hyomandibular extends beyond this articulation and is firmly fixed to the quadrate. Only by breaking this lamella could one move the hyomandibulo-quadrate articulation. Such are the relations found in the small specimen of *Eurypharynx* which I studied. As already mentioned, all earlier writers describe this articulation as highly mobile (Nussbaum-Hilarowicz, pp. 56–57), and consider the mobility of the hyomandibulo-quadrate articulation as one of the important characteristics of the order Lyomeri (Regan, 1912 *a*, p. 348). Bertin (1934, fig. 1) illustrates the movements of this articulation. It seems, however, that the position of the upper jaw, of the hyomandibular, and of the quadrate shown on his figure, could not be achieved without breaking the bones concerned.

The quadrate is markedly longer than the hyomandibular and consists of a long, well-ossified rod which appears as a direct prolongation of the main rod of the hyomandibular; the cartilaginous upper end of the quadrate articulates with the hyomandibular; its lower end is received into the groove of the mandible. The head of the quadrate articulating with the mandible is of a complicated structure (a double rotatory diarthrosis), and bears processes, one medial (inner) and one lateral (external).

The mandible is long, thin and rod-like. In the specimen which I studied, at about the middle of the mandible its sectional diameter is only about 0·25 mm., while the length of the mandible is 36 mm. So it is about 144 times as long as it is broad, or deep. It is well ossified along its whole length. Meckel's cartilage is very much reduced and restricted to the posterior part of the mandible. In the specimen studied by me Meckel's cartilage is about 6 mm. long ($\frac{1}{6}$ the length of the mandible). 11/12 of the mandible form a tube ossified all round, and only the posterior 1/12 is open from above and boat-shaped. The posterior tip of the mandible extends behind the mandibulo-quadrate articulation, and turning upwards is received between the two articulating discs of the quadrate. Into this posterior tip of the mandible a tendon of the *m. abductor mandibulae* inserts. The greater part of this tendon is ossified into a long bone lying along the dorsal (posterior) side of the quadrate.

Numerous small teeth are set in two rows along the mandible from its tip nearly to its posterior end. The dentigerous surface is not along the dorsal, but along the medial side of the mandible. Thus, except for its posterior part, the mandible is a long narrow cylinder *ossified on all sides*. The posterior part of the mandible in front of the articulation with the quadrate is of different structure. Its dorsal surface is open and exposes the narrow Meckelian cartilage, which also extends somewhat further forwards into the tube-like part of the bone. Both sides of the posterior part of the mandible are elevated by two rising lamellae. The inner

(medial) lamella is very short, the outer (lateral) is markedly larger and serves for the attachment of the ligaments of the main parts of the *m. adductor mandibulae*. This muscle has no part extending into the mandible and is not inserted into the Meckelian cartilage.

When the mouth is shut, the boat-shaped posterior part of the mandible receives the posterior end of the quadrate with that of the bone forming the upper jaw.

The anterior ends of the rami of the mandible articulate firmly together. Their union is strengthened by an azygous cartilage covering the symphysis from in front. This articulation is movable, hinge-like, as this articulation usually is in fishes; it certainly is not 'loose' (comp. Regan, 1912 a, p. 348).

The ossified parts forming the mandible are apparently fused together, and no junction between them could be found in the specimen which I studied (*cf.* p. 331, the mandible of *Saccopharynx*). The bone bears no sign of enclosing the mandibular sensory canal. The mandibular branch of the lateral line system is apparently absent in Lyomeri (p. 323).

Synonymy. Nussbaum-Hilarowicz (1923, p. 58) limits his description of the lower jaw of *Eurypharynx* by a negative statement that articulare, dentale and angulare are absent, and does not mention of what elements the lower jaw consists. Bertin (1934, p. 4) confirms this statement and adds (p. 7) that the skeleton of both jaws consists of cartilage. According to Regan (1912, p. 348) the lower jaw of Lyomeri consists 'of dentary, articulare and augulare'.

The upper jaw. The bone playing the rôle of the upper jaw is slightly shorter and markedly thinner than the mandible. The anterior end of each of its rami widens and articulates with its fellow under the vomer. The tips of both rami are attached by a strong and broad ligament to the ventral side of the cranium. This ligament extends forwards along the anterior part of the vomer up to the tip of the rostral cartilage. The articulation is movable as far as the elasticity of tissues permits it. The position of this ligament and of the upper jaw shown on Bertin's (1934) figures 12 and 35 can be achieved only by tearing off the tissues attaching the ligament to the ventral side of the cranium, of the mucous membrane of the mouth, and of the skin on the ventro-lateral side of the rostrum.

When examined under a microscope, the upper jaw bone appears as consisting of two longitudinal parts fused together, a narrow tube widening anteriorly, and a flat lamella, broader than the tubular part, situated ventrally to the latter. At the posterior end, the lamelliform part becomes gradually narrower and disappears, while the tubular part becomes thinner and passes into a softer tissue which may be a ligament or a cartilage (not stained by alizarin in the clarified specimen). It attaches itself by ligaments to the inner surface of the quadrate and has possibly a ligamentous attachment within the mandible (compare p. 331). The teeth are numerous, set in two rows along the medial surface of the bone, where the tubular and the lamelliform parts meet. The teeth-bearing surface extends along the whole ossified part of the upper jaw. The teeth situated in this way face each other in both rami. The bone is not enclosed in a cutaneous fold; its anterior part is possibly associated with the infraorbital branch of the lateral system (p. 322).

The teeth of *Eurypharynx* are small and to the naked eye appear as thin granulations. With magnification one can see that each tooth consists of a thin, scale-like basal plate and a sharp cone projecting from it; the cones are curved pointing into the mouth cavity. The basal plates of the teeth are set close together. In preserved specimens the teeth fall out at the slight touch of a needle to the basal plate; the teeth are not co-ossified with the bone of the jaw.

Gill and Ryder (1883, 1884) and Gill (1883) considered the upper jaw of *Eurypharynx* as the palatine; Gill and Ryder (1884, foot-notes on pp. 60, 61) and Günther

(1870, 1887) as maxillary; Zugmayer (1913) and Bertin (1934) as maxillaire; Nussbaum-Hilarowicz (1923) as maxilla; Regan, 1912 *a*, as praemaxillo-maxillary.

The skeleton of the branchial arches has never been studied, and the little that is known about it is described on p. 306.

On the homology of the visceral skeleton of Eurypharynx.—The visceral apparatus of *Eurypharynx* with its six functional visceral clefts and five holobranchs is unique among living fishes having true bones, but as the morphology of *Eurypharynx* is imperfectly known, and its development has never been studied, the nature of this feature is not certain and can be differently interpreted.

It seems generally preconceived * that the five anterior visceral clefts and the four anterior holobranchs of *Eurypharynx* are homologues to the five branchial clefts and to the four holobranchs of Actinopterygians, and that *Eurypharynx* has an additional, posterior, sixth cleft (never found in living or extinct Actinopterygians). Thus, one has to suppose that the posterior holobranch of *Eurypharynx* is formed by the posterior hemibranch of the fifth pouch and by the anterior hemibranch of the sixth pouch (a hemibranch never found in any Actinopterygians) †. It is also generally agreed that, contrary to all other fishes, *Eurypharynx* has only one hyoid element, which is the hyomandibular. This point of view was accepted without any discussion, and no doubts arose that it might not be correct. However, the homologies of the elements concerned may be quite differently interpreted.‡

It seems possible that the ventral parts of the hyoid arch of *Eurypharynx* are not missing, and are found in the septum behind the anterior visceral cleft. If so, this cleft is the mandibulo-hyoid (prehyoid) cleft, and the next five clefts are homologues to the five branchial clefts of fishes; the first holobranch is formed by the posterior hemibranch of the mandibulo-hyoid pouch and by the anterior hemibranch of the pouch between the hyoid and first branchial arches; it would thus correspond to the gill of the hyoid arch of Acanthodians as described by Watson, 1937, and not to the gill of the first branchial arch of Actinopterygians; the four next holobranchs would be homologous with the holobranchs of Actinopterygians. The posterior hemibranch of the fifth pouch would be missing in *Eurypharynx*, as it is always missing in Actinopterygians.

Which of these two interpretations is more likely to be correct? Let us discuss the homologies of the other visceral elements of *Eurypharynx*. What is in *Eurypharynx* the proximal element of the suspensorium, which is described as the hyomandibular? Is it a hyoid element, or a separate element of the palato-quadrate?

The structure of this element in *Eurypharynx* differs much from the typical hyomandibular of Actinopterygians; it has no opercular process and no operculum is attached to it; it articulates directly with the distal element of the suspensorium, and consists of a rod-like ridge and a lamelliform part joined to it.

An examination of the cephalic nerves (p. 313) of *Eurypharynx* shows, however, that the *r. mandibularis internus* of the facial nerve passes through the foramen in the proximal element of the suspensorium and thus this element in *Eurypharynx* is homologous with the hyomandibular of Actinopterygians. Therefore, if the suggestion that the foremost visceral cleft of *Eurypharynx* corresponds to the ventral part of the mandibulo-hyoid cleft is correct, one can expect to find a reduced number of skeletal elements in the septum behind this cleft. Unfortunately their number is not known. Only Nussbaum-Hilarowicz examined the cartilages in the visceral septa of *Eurypharynx*. He found 'three or four' cartilages in these septa but he did

* Except by those writers who overlooked this main character of *Eurypharynx* (Günther 1887, p. 262; Zugmayer, 1911, p. 348; 1913, p. 4; Regan, 1912 *a*, p. 348; 1925, p. 57).

† The statement that *Polyodon* has 4½ gills (Günther, 1880, p. 362, and some others) has been proved to be incorrect (Rauther, 1935, pp. 61, 62; 1937, p. 243).

‡ See note on p. 287.

not even say in which of these septa he found three and in which four cartilages. (The course of the *ramus hyoideus* of the facial nerve in *Eurypharynx* is described on p. 315.)

The upper jaw.—The bone forming the upper jaw of *Eurypharynx* is usually considered as maxillary or premaxillo-maxillary, and it is usually supposed that the palato-pterogoid elements are completely absent in *Eurypharynx*; if so, the dorsal part of the mandibular arch consists of a single rod-like element corresponding to the quadrate and the mandibular arch does not articulate with the neurocranium at all (text-fig. 15 A). However, the medial position of this bone to the *m. adductor mandibulae*, the attachment of this bone to the medial side of the quadrate and of the mandible, give ground for the suggestion that it is a palato-pterygoid element, and that the maxillary and premaxillary are absent in *Eurypharynx* (p. 311). In text-fig. 15, A, B, the two ways of interpreting the visceral elements of *Eurypharynx* are shown graphically.

The preoperculum, the opercular bones and the branchiostegals are completely absent in *Eurypharynx*. Most of the writers on Lyomeri believe that the absence of these elements, though unique among living fishes, is of little importance, and only Nussbaum-Hilarowicz (1923, p. 74) considers this character as of primary significance and believes that on this ground the Lyomeri can be opposed as a distinct group to all other fishes.

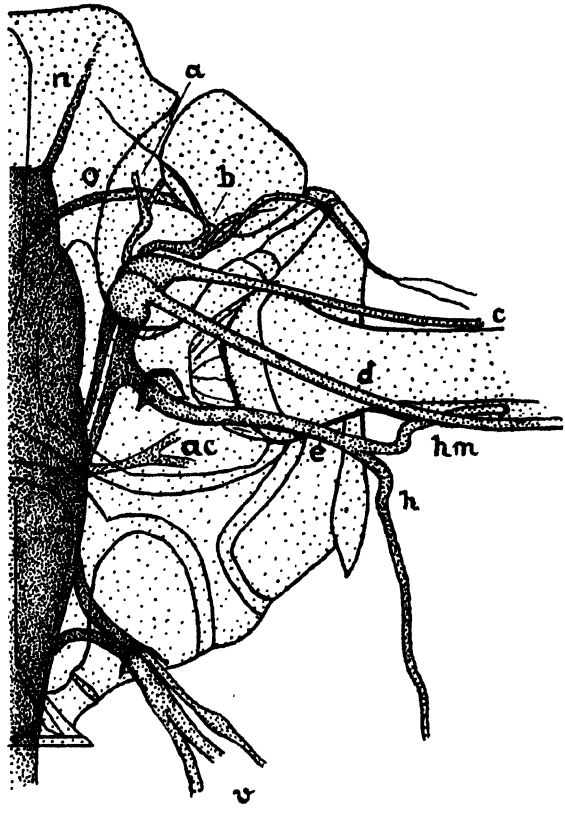
On the cephalic nerves of Eurypharynx.- A study of the vascular and nerve systems could give a key to the homology of the visceral skeleton of *Eurypharynx*. But the vascular system of Lyomeri has never been studied, and very little is known about its nerve system. Nussbaum-Hilarowicz (1923, pp. 68–70, pl. ix) described and figured the cephalic nerves of *Eurypharynx* but he did not show the relation of the nerves to the visceral arches. The material in hand excludes the possibility of an examination of the blood-vessels and only very little can be done about the cephalic nerves.

The results, which I obtained by examining the specimen of *Eurypharynx* in hand, can thus be summarized (text-fig. 8).

Trigeminus-facialis group.—Two roots originate from the side of the hind brain. The posterior of these roots appear to be subdivided into two, but this subdivision is not clear, and is not shown in the figure. A compound trigemino-facialis ganglion is situated in the anterior groove of the prootic (compare Nussbaum-Hilarowicz, 1923). Five divisions of this ganglion can be recognized. They are shown on text-fig. 8 and marked by letters *a*, *b*, *c*, *d*, *e*.

The division *a* corresponds probably to the *n. ophthalmicus superficialis*; it originates from the main ganglion, has a short run and divides in the orbit into two branches. The division *b*, which apparently is the *n. ophthalmicus profundus*, leaves the main ganglion laterally to the division *a*, passes laterally into the orbit, and divides into three branches; the anterior one passes towards the rostrum, the medial towards the eye ball, and the posterior, a much longer one, passes into the muscle extending along the suspensorium. This posterior branch runs dorsally to the *r. maxillaris trigemini* (*c* in the figure). The division *c*, which probably is the *r. maxillaris trigemini*, passes straight into the ventro-anterior side of the *m. adductor mandibulae* and runs along the anterior edge of the suspensorium to the distal end of the quadrate, where the nerve is torn off. Thus, it is not clear what happens to it when it reaches the articulation of the quadrate with the upper and lower jaws. The division *d*, which probably is the *r. mandibularis trigemini*, issues from its own part of the ganglion and passes towards the ventro-posterior side of the suspensorium; it runs along

the posterior side of the suspensorium to the mandibulo-quadrate articulation, where this nerve is also torn off. The fifth division *e*, which apparently corresponds to the *truncus hyomandibularis* of the facial nerve (compare Nussbaum-Hilarowicz, 1923), diverts from the posterior part of the complex *trigemino-facialis* ganglion, passes backwards and outwards through a canal in the prootic (which is possibly also the jugular canal) and then extends laterally towards the hinder edge of the suspensorium. It divides soon into two branches. One turns sharply towards the rostrum, reaches the hind edge of the suspensorium, turns again at a right angle laterally, and after a short run along the hind edge of the suspensorium (dorsally to the *ramus mandibularis trigemini*), enters (from the medial side) the lamelliform part of the



TEXT-FIG. 8.—Cranial nerves of *Eurypharynx pelicanoides*. Diagram of the left side of the neurocranium. Ventral view. ×10. Drawn from a clarified skull (specimen 'Discovery' st. 287). The brain and the nerves seen through the transparent elements of the skeleton are shadowed dark grey; nerves outside the skull pale grey; elements of the skeleton sparsely dotted.

a, *n. ophthalmicus superficialis*; *ac.*, *n. acusticus*; *b*, *n.ophthalmicus profundus*; *c*, *r. maxillaris trigemini*; *d*, *r. mandibularis trigemini*; *e*, *truncus hyomandibularis* of the facial nerve; *h.*, *ramus hyoideus* of the facial nerve; *hm.*, *ramus mandibularis internus* of the facial nerve; *n.*, *n. olfactorius*; *o.*, *n. opticus*; *v.*, nerves of the *vagus* group. For the parts of the skeleton compare Pl. 8, fig. 2.

hyomandibular, passes through it, and extends along the posterior edge of the suspensorium following closely the division *d* (*r. mandibularis trigemini*) to the mandibulo-quadrate articulation, where this nerve is also torn off; the course of this branch suggests that it is the *r. mandibularis internus* of the facial nerve. The second branch of this division, *e*, turns sharply backwards towards the gill apparatus, but I could not see its relation to the foremost visceral cleft. By its position it may correspond to the *r. hyoideus* of the facial nerve. If so, the fact that the *r. hyoideus* is well developed, suggests that the muscles innervated by this nerve are functional and does not agree with the idea that the ventral hyoid elements of *Eurypharynx* are missing. The sharp caudalwards turning of this nerve suggest also that in *Eurypharynx* one has to look for the ventral hyoid elements somewhere well behind the hyomandibular.

A nerve (*ac.*) which is probably the acoustic nerve, originates behind the *trigemino-facialis* roots, it divides into two short branches, none of which passes out of the skull (compare Nussbaum-Hillarowicz, 1923, p. 70, pl. ix, fig. 1).

The vagus group (*v.*). The roots of the *n. glosso-pharyngealis* and of the *n. vagus* are very distinct, both nerves pass through a single foramen in the lateral occipital. Within the cranial case the root of the *n. vagus* runs first forwards and then turns laterally and backwards forming an arch. In the specimen which I studied both these nerves are torn off close to the neurocranium, and their course and relation to the visceral arches could not be examined.

Summing up.—The present examination of the visceral nerves of *Eurypharynx*, unsatisfactory as it is, shows: (1) that the proximal element of the suspensorium, crossed by a branch of the facial nerve, is the hyomandibular; (2) that there is some reason to hold that the ventral hyoid elements of *Eurypharynx* exist, for a branch of the *truncus hyomandibularis* (vii), which is probably the *r. hyoideus*, is strongly developed; (3) that the ventral hyoid elements, if present, are situated well behind the suspensorium. Thus there is some ground for the suggestion that the anterior visceral cleft of *Eurypharynx* is a mandibulo-hyoid cleft, and that the arch behind it corresponds to the ventral elements of the hyoid arch *.

I shall return to the homologies of the visceral elements at the end of this paper when the relationship of Lyomeri is discussed.

(b) *The Neurocranium* (Pl. 3, figs. 1, 2; text-fig. 8). The *chondrocranium* is largely unossified, and the primordial cartilage has no divisions in places corresponding in position to the supra-occipital and to the lateral ethmoids of other fishes. The structure of the roof of the primordial cranium is unknown. It has not been described previously, and during this study the cover bones lying on the dorsal side of the neurocranium could not be removed. Parts of the neurocranium are movably united with one other and it can thus noticeably change its shape. The interorbital part is very low, and there is no myodome. The cranial case is large in proportion to the size of the neurocranium. The brain extends forwards right into the orbital region (text-fig. 8).

In text-fig. 8 the position of the brain in the cranium is shown. The neurocranium has not been dissected, but only clarified (and the bones stained), so the position of the brain has not been affected by dissection. The roots of the optic nerves (*o.*), hidden under the vomer heavily stained with alizarin, could not be seen clearly.

The otic region expands very much anteriorly, the prootics extend forwards into the cartilage of the interorbital septum beyond the hypophysis. There are no grooves for the olfactory organs in the ethmoid cartilage.

* See note on p. 287.

The occipital region (Pl. 3, figs. 1, 2) consists of three elements only : two lateral occipitals and a basioccipital. The *foramen magnum* is surrounded by these three elements. *There is no supraoccipital.* The outer foramen of the *n. vagus* is on the ventral side in the posterior part of the lateral occipital (Pl. 3, fig. 2). According to Gill and Ryder (1883, p. 264), ' the notochord is persistent in the skull for half the length of the basioccipital '. I could see only a small part of the notochord, filling the space between the concave articulating surfaces of the basioccipital and the first vertebra. But I did not disjoin the skull from the first vertebra.

The absence of the supraoccipital.—I examined the occipital region and the roof of the cranium of *Eurypharynx* under a microscope with strong reflected and transmitted light from a Leitz Monla lamp, and could not find any trace of the supraoccipital (ossified or cartilaginous). In the specimen examined there is a space which is unossified between the upper parts of the two lateral occipitals ; this is a part of the cartilage-roof of the primordial cranium which extends forwards between the epiotics, and further forwards, up to the ethmoid rostrum, without any interruption or division. Nowhere along the medial line of the chondrocranium has alizarin stained it, though all the smallest ossifications of the skull are clearly stained (Pl. 3, fig. 1). (The absence of the supraoccipital in Lyomeri is confirmed by the study of a much larger specimen of *Saccopharynx* ; see p. 332, Pl. 3, fig. 3.)

The fact that a supraoccipital ' *bone* ' has been described by the earlier writers seems likely to be the result of their conviction that a supraoccipital must be present in all ' teleosteans '. However, all ichthyologists described the supraoccipital differently in this fish. According to Gill and Ryder (1883, p. 264), it is a ' very small transverse bone *above the foramen magnum* and *protruded forward as a triangular wedge between the two parietals* ', *i. e.*, according to Gill and Ryder, the supraoccipital is found on the dorsal side of the skull. Contrary to this, Zugmayer (1913, p. 5) figures a ' supraoccipital ' as a *forked bone* with its apex articulating with the epiotics (' parietals ' *auctorum*) and *with its two branches extending downwards* along the sides of the *foramen magnum, i. e.*, according to Zugmayer, the supraoccipital lies in the posterior wall of the skull. Regan (1911, p. 348, fig. A) shows a ' supraoccipital ' as a very small *rounded element* situated above the *foramen magnum*. However, Dr. Regan had no opportunity of examining the skull of *Eurypharynx* himself, and his figure is made from an earlier figure of Zugmayer's (1911, pl. iv, fig. 3 *c*), which is more artistic than exact or clear, and where no limits between the bones and cartilage are shown.

Only Nussbaum-Hilarowicz (1923, p. 55, pl. viii, fig. 2), who carefully studied three skulls of rather large *Eurypharynx* using different methods, could not find a supraoccipital in *Eurypharynx*. Bertin (1934, p. 18, fig. 10) took an average line, notifying in his text the presence of a ' supraoccipital ' (' très petit '), does not show it on his figure nor mention it in the legend to this figure. However, his figure was made ' en partie d'après Nussbaum-Hilarowicz, Regan et Zugmayer ', who all disagreed on the subject of the supraoccipital of *Eurypharynx*.

Eurypharynx is not unique among the Actinopterygii in having no supraoccipital. Besides *Polypterus*, *Acipenser*, *Amia* and *Lepidosteus*, the supraoccipital is missing in several ' true teleosteans ' : *Nematoprora polygonifera*, *Serrivomer beani* (Trewavas, 1932, pp. 648, 650, pl. ii, fig. A. pl. iii, fig. A), and in *Cyema atrum* (Trewavas, 1933, p. 602, pl. i, fig. A). I had the opportunity of examining the excellent specimen of *Cyema* clarified and stained with alizarin by Dr. E. Trewavas. It can be distinctly seen in this specimen that the supraoccipital (ossified or cartilaginous) is completely absent.

The basioccipital (Pl. 3, figs. 1, 2 *B.*) is a large bone extending to slightly more than a third the length of the ventral surface of the skull. It is rather well ossified,

but its lateral and anterior edges on the ventral surface are cartilaginous. The basioccipital projects backwards considerably beyond the vertical line drawn at the dorsal edge of the *foramen magnum*; the lateral edges of this aperture, formed by the lateral occipitals, slant down and backwards, so that the *foramen magnum* can be well seen from above (Pl. 3, fig. 1). The posterior part of the basioccipital is very like a vertebra (see p. 33); it ends in a rounded facet for articulation with the anterior ringlike facet of the first vertebra. Through these two facets passes the anterior end of the notochord.

Nussbaum-Hilarowicz does not describe the articulation of the skull with the first vertebra, but shows in his figures (pl viii, figs. 1, 2) a convex articulation facet on the posterior end of the basioccipital with a small groove in its centre. This is not the case in the specimen of *Eurypharynx* which I examined; and is not found in *Saccopharynx*.

The basioccipital has two short dorsal processes, which articulate with the lower ends of the lateral occipitals by synchondrosis. This articulation is movable. (More details of this articulation are given in the description of *Saccopharynx*, p. 333.) Two longitudinal thin apophyses rise ventrally at the sides of the posterior edge of the basioccipital, and extend forwards along its ventral surface towards each other; they join together at the medial line, and extend further forwards forming a ridge continued to the fore edge of the basioccipital. This ridge is quite independent of the parasphenoid, the posterior part of which lies under this ridge.

On the ventral side, the basioccipital does not articulate with the prootics immediately, and a narrow strip of primordial cartilage divides these bones. The basioccipital articulates with the lateral occipitals by harmony. These two articulations allow some movement between the elements concerned, owing to the elasticity of the intermediate cartilage.

Synonymy and homology. Only Gill and Ryder (1883) described the basioccipital correctly. The antero-ventral part of this bone was later erroneously described as a separate bone and confused with the parasphenoid and even the basisphenoid. ('Sphenoide', Zugmayer, 1911; 'sphenoide=parasphenoideum', Zugmayer, 1913; 'basisphenoideum', Nussbaum-Hilarowicz, 1923; Bertin, 1934. The latter writer considers only the posterior facet of the basioccipital as a 'basioccipital'; all the rest of this bone, according to his terminology, is a '*basisphenoide*'.)

The lateral occipitals (Pl. 3, figs. 1, 2, *L.*) surround from the sides and partly from above the *foramen magnum*. Dorsally they articulate by means of a cartilaginous bridge with the epiotics and dorsally and ventrally with the endochondral part of the pterotics. A large aperture for the nerves of the *vagus* group is found on the ventral surface at the hind edge of each lateral occipital. According to Gill and Ryder (1883) 'the foramen for the passage of the ninth and tenth nerves opens alongside the basioccipital and perforates the exoccipital' (see also Nussbaum-Hilarowicz, 1923, p. 70, pl. ix, fig. 1; and text-fig. 8 of this paper).

The otic region.—The structure of the auditory organs of Lyomeri has not been studied, and their relations to the bones of the occipital and otic regions are unknown. Thus the homologies of the elements of the otic region are rather uncertain. No otholits could be seen in the clarified specimen examined by me.

The otic region contains five pairs of cartilage-bones; the pterotics ('opisthotics' of Holmgren and Stensio, 1936), the epiotics, the sphenotics and the prootics. There are no opisthotics (see p. 318), no alisphenoids and no basisphenoid. The prootics expand anteriorly more than is usual; they extend forwards ventrally into the interorbital region beyond the trigeminus ganglion and beyond the hypophysis. The epiotics cover about the whole of the posterior half of the roof of the cranium.

The pterotics (Pl. 3, figs. 1, 2, *PT.*).—The pterotics form the posterior-lateral edge of each side of the cranium. Each pterotic is fused with a dermal pterotic (the intertemporal-supratemporal or supratemporal bone) related to the posterior part of the temporal section of the infraorbital lateral line canal, forming thus the compound bone usually called 'pterotic'. It articulates (by synchondrosis) ventrally with the lateral occipital and epiotics, and anteriorly with the sphenotic. It forms (ventrally) the posterior lateral part of the groove for the articulation with the condyle of the hyomandibular. The cartilage-pterotics are exceptionally large in Lyomeri.

All writers on Lyomeri described and figured a separate element between the pterotic and the lateral occipital; Gill and Ryder (1883) call it opisthotic; Nussbaum-Hilarowicz,—opisthoticum; Zugmayer (1911, 1913),—occipital externe=epioticum; Regan (1912 *a*),—epiotic; Bertin (1934, pp. 18, 19),—opisthotique (on p. 4 he denies the existence of the 'opisthotique' in all Lyomeri). From Nussbaum-Hilarowicz's figures (pl. viii, figs. 1, 2) this element articulates with all the surrounding bones (including the pterotic, which according to Nussbaum-Hilarowicz's terminology is a 'prootic') by means of narrow cartilage-bridges. According to Nussbaum-Hilarowicz, this element extends ventrally more than dorsally and articulates with the prootic ('alisphenoideum' of Nussbaum-Hilarowicz).

If the element described by these writers really existed, the Lyomeri would be the only known fishes with a real cartilage-opisthotic not fused with any other cartilage-bones or with the dermal intercalary. However, I could not find any trace of such an element in the specimens examined (*Eurypharynx* and *Saccopharynx*). To avoid misunderstanding, I would like to add here that Lyomeri *have no secondary intercalary*, which is often also called 'opisthotic'. There is much confusion about the opithotic and the intercalary in the literature, but I do not intend here to go into details on this problem (see Bruch, 1861, p. 7; Huxley, 1871, p. 153; Günther, 1880, p. 56; Holmgren and Stensio, 1936, p. 491; and especially de Beer, 1937, pp. 87, 130, 150, 160, 164, 167, 497).

The prootics (Pl. 3, fig. 2, *P.*).—The prootic is a large and well-ossified bone. It articulates with its fellow along the medial line of the floor of the chondrocranium by a cartilage-bridge. It articulates by synchondrosis with the pterotic, the lateral occipital, and the basioccipital. The elastic cartilage uniting these bones permits some movement between them. The prootic sends forward and downwards a conical process or flange which articulates synchondrosically with the ventral lower end of the sphenotic (autosphenotic, Holmgren and Stensio and de Beer). This articulation is clearly a movable one. The outer side of the prootic is deeply grooved, forming a part of the depression for the condyle of the hyomandibular. The prootic sends downwards a thin semi-lunar lamella which overlaps medially the condyle of the hyomandibular; and deepens thus the articulating groove. The anterior (orbital) edge of the prootic is deeply recessed forming a semi-open trigemino-facialis chamber. The hyomandibular branch of the facial nerve passes out through a foramen in the prootic posteriorly to the trigeminus facialis ganglion. As there is no alisphenoid and no basisphenoid, the trigemino-facial chamber is not closed anteriorly. According to Nussbaum-Hilarowicz (1923, pp. 5, 70, pl. viii, fig. 2; pl. xi, fig. 1) the prootic has three foramina for the branches of the *n. trigeminus* (p. 55), and has a separate foramen for the *n. facialis* (compare p. 313 of this paper and fig. 8).

Synonymy.—Gill and Ryder (1883) 'probably prootic'; Zugmayer (1913) aile du sphénoide=prooticum; Nussbaum-Hilarowicz (1923) alisphenoideum—not prooticum; Bertin (1934), alisphenoide.

The sphenotics (Pl. 3, figs. 1, 2, *S.*).—The sphenotic is well ossified and forms the posterior lateral edge of the orbit and ventrally takes part in the formation of the

articulating groove for the hyomandibular. The dorsal part of the sphenotic articulates with the parietal, frontal, and the pterotic. The shape and the relief of the dorsal part of the sphenotic suggest that it is a dermal ossification, connected with the sensory canal system, and seems thus to correspond to the dermal sphenotic (intertemporal). But there is not enough evidence for such a conclusion. The ventral part of the bone is more solid and is deeply embedded in the cartilage. It forms a process or flange growing downwards and backwards to meet a similar process from the prootic. They articulate movably by a small cartilage situated between them.

Synonymy and homology.—Gill and Ryder (1883) and Zugmayer (1911, p. 93) apparently did not find this element in *Eurypharynx*, but later Zugmayer (1913, p. 2) mentions a frontal postérieur=sphenoticum. It is clear, however, from his figure (p. 5) that he applied this name to the whole of the primordial cartilage of this region, and probably did not see the bone itself. The same can be said about the figure of Nussbaum-Hilarowicz (pl. viii, figs. 1, 2, p. 55). He marks as 'sphenoticum' the cartilage at the hind edge of the orbit, and considers the ventral process of the sphenotic as the 'orbitosphenoideum'. According to Nussbaum-Hilarowicz, there are two orbitosphenoids which are widely separated from each other not only by the interorbital cartilage but also by the prootics. Bertin (1934, pp. 18, 19) follows this unusual nomenclature.

The epiotics (Pl. 3, fig. 1, *E.*) By their position and shape the epiotics of *Eurypharynx* recall those of some Ceratioidea, as, for instance, those of *Trematorhynchus leucorhinus* (see Regan and Trewavas, 1932, fig. 45). Each epiotic is a large, rather flat bone embedded in the primordial cartilage of the cranial roof. It articulates medially with its fellow by synchondrosis, joining in a similar way with the lateral occipital and the pterotic. Anteriorly it is narrowly, but distinctly, separated from a dermal bone which may be the parietal. It seems possible that this distinct separation of the epiotics from the parietals is due to the small size of the specimen studied, and that in larger specimens the edges of these bones join by synostosis, and their boundary becomes less distinct.

Synonymy.—All earlier writers figure the epiotic and the parietal as a single bone (on each side of the skull) and describe them as 'large parietals' (cf. *Saccopharynx*, p. 334).

The orbital region (text-fig. 8, Pl. 3, figs. 1, 2).—The eye of *Eurypharynx* is small and hidden below the transparent skin. Its function is probably much reduced; the eye muscles are short and weak. The eyes are divided from each other by the broad and flat interorbital cartilage (Pl. 3, fig. 2, *C.*) and by the anterior medial processes of the prootics embedded in this cartilage. There is no orbitosphenoid. The eye-balls have little skeletal protection from above or from in front. There are no *sclerotic bones.*

The basisphenoid and *alisphenoids* are absent (Pl. 3, fig. 2). There is no posterior myodome. The *m. recti* arise from the side of the flat interorbital cartilage close to the front edge of the prootic, and the *m. obliqui* apparently from the same cartilage near the anterior edge of the orbit (*cf.* p. 334). The brain case extends anteriorly beyond the orbital region dividing the eyes from each other; the interorbital cartilage (*C*) floors this case. Dorsally the brain case, above the orbital region, is covered by the cartilaginous roof of the chondrocranium strengthened by the dermal plates which are probably the frontals; they extend anteriorly and also cover almost entirely the short rostrum (Pl. 3, fig. 1).

The ethmoid region.—The ethmoid region in *Eurypharynx* (Pl. 3, figs. 1, 2) is short and blunt; it contains no cartilage bones. There are no grooves for the olfactory organs. The lateral ethmoids are absent. The canals for olfactory nerves perforate this cartilage and open at the anterior lateral edges of the *rostrum* (Pl. 3, fig. 8) under the small nasals (Pl. 3, fig. 1, *N.*). The nasals are dermal ossifications related to the supraorbital sensory canal.

There is no supra-ethmoid (*rostrale-postrostrale* Holmgren and Stensio).

Synonymy and homology.—There is some confusion about the nomenclature of the elements of the ethmoid and orbital regions; some of the elements, absent in *Eurypharynx*, have been described as present; or the names of the absent elements of these regions have been wrongly applied to other elements. To avoid further confusion I give here a brief list of these names:

The ethmoid or mesoethmoid.—Gill and Ryder (1883) give the name 'ethmoid' to the rostral cartilaginous part of the cranium (which, according to Zugmayer, Nussbaum-Hilarowicz, and Bertin is a 'nasale'). Zugmayer (1911, 1913) showed in his figures a bone situated in front of the frontals, which, narrowing anteriorly, covers the ethmoid cartilage. He called this bone 'ethmoide=mesoethmoideum'. Zugmayer figures the frontals as square bones, their anterior edges forming a straight line across the skull. It is quite clear, however (in the specimen I studied), that the frontals are triangular, and, narrowing anteriorly, cover the ethmoid region of the skull.

I could find no trace of the supra-ethmoid in *Eurypharynx*. Regan (1912 *a*), Nussbaum-Hilarowicz (1923) and Bertin (1934), relying apparently on Zugmayer's figure, showed an 'ethmoid' similar to that figured by Zugmayer. Regan (p. 348) and Bertin (p. 19) admit themselves that their figures are made after Zugmayer's drawing.

Lateral ethmoids were not mentioned by Gill and Ryder (1883), Zugmayer (1911) or Regan (1912 *a*), but Zugmayer (1913) named the whole of the ventral non-differentiated rostral and interorbital cartilage from the anterior end of the vomer to the prootic—'frontal antérieur = ethmoideum laterale'. Nussbaum-Hilarowicz (1923) followed this regrettable example, and Bertin (1934) copied it also.

Basisphenoid.—Zugmayer (1913) named thus by error the anterior part of the basioccipital. Nussbaum-Hilarowicz and Bertin followed this nomenclature.

Alisphenoids.—Name erroneously used by Nussbaum-Hilarowicz, and after him by Bertin, for the prootic.

Orbitosphenoids.—Nussbaum-Hilarowicz, and after him Bertin, erroneously used this name for the ventral parts of the sphenotics (autosphenotic Holmgren and Stensio, and de Beer).

Cover bones on the ventral side of the neurocranium (Pl. 3, fig. 2). *Vomer* (*V.*) (=prevomer, de Beer, 1937) is a narrow, thin bone. It extends from near the tip of the snout to more than a third the length of the skull. It is broader in front and narrows gradually posteriorly. It has no teeth, and no contact with the cartilage.

The parasphenoid (*PS.*) is also narrow, long and thin, its anterior end does not quite reach the posterior end of the vomer; it extends backwards to about the place where the ventral processes of the basioccipital join together forming a single ridge. The parasphenoid has no lateral wings (*processus ascendens*). It has no apertures for the carotids or nerves. There is apparently no space between the ridge of the basioccipital and the parasphenoid. In the small specimen studied by me, the vomer and the parasphenoid are separated by a considerable space, but it is possible that in larger specimens these bones join together, or overlap each other.

Synonymy and homology.—Gill and Ryder (1883): 'There is no vomer'; 'The parasphenoid is present and extends as a narrow splint from the hinder portion of the

basioccipital to very near the end of the rostrum '. Zugmayer (1911, 1913) shows the vomer extending over the anterior part of the basioccipital; he shows no parasphenoid in his figure, but by his terminology the anterior ventral part of the basioccipital is a 'sphénoide' which, according to Zugmayer, is a synonym of the 'parasphenoideum'. According to Nussbaum-Hilarowicz, the 'sphénoide=parasphenoideum' of Zugmayer, is a basisphenoideum, which is not a parasphenoideum, and the true parasphenoideum is absent in *Eurypharynx*; but according to Bertin's ideas (p. 18) the ventral surface of the *basioccipital* is a 'basisphénoide' which is exactly the same as the 'sphénoide', and again the 'sphénoide' is the same as the 'parasphénoide'. One can only wish that such nomenclature should not be used.

(c) *The lateral line system of Lyomeri and the bones connected with this system.*—The lateral line system is in many cases the only guide to the homology of some of the cover bones in fishes, and deserves careful study. In Lyomeri this system is unusual. It consists of 'tubules' or papillae, several millimetres long, projecting from the skin. The papillae are single or grouped together (groups of two in *Saccopharynx*, and 4–5 in *Eurypharynx*), and are arranged in longitudinal series. The position of the series recalls generally that of the mucous canals of fishes.

Only the external structure of the papillae and their disposition along the head and body have been described. It has not been shown where the sensory organs are located, how innervated, or even whether the sensory organs are present or not. The mucous canals of the system have not been described.

However, the opinion seems generally adopted that this system in Lyomeri is a real lateral line system. This view is supported by the fact that a lateral line system with similar projecting papillae has been found in two other groups of deep-sea fishes, and in those fishes it has been proved that it is a real lateral line system and is connected with the cover bones. (Ceratioidea, Regan and Trewavas, 1932, pp. 23, 24, figs. 16–18, pls. vii, viii; and *Cyema* Brauer, 1906, p. 131, pl. viii, fig. 3; Trewavas, 1933, pp. 601–602).

The Lyomeri preserved in the British Museum are not in a sufficiently good condition for the study of the minute structure of the lateral line system. Even the general disposition of the series of this system is not always clear, as the skin on the heads of the specimens is broken.

The examination of these specimens is useful only for comparison with the earlier descriptions.

The results of the study of literature and of the specimens of the British Museum can be thus summarized.

Structure of the papillae.—Agassiz (1888, pp. 35–36) describes the papillae of the lateral line of *Eurypharynx* as stalked organs more or less cup-shaped. In *Eurypharynx* each papilla (examined under a microscope) appears as a cylinder with very thin transparent walls, apparently continuous with the epithelium of the skin. The apex of the papilla expands slightly, and has a kind of a white crown. Inside the papilla a white thread extending from its apex to its foot can be seen. At the base of each papilla (or of each group of papillae) the skin forms a whitish disc. (According to Bertin, 1934, p. 14, the papillae are empty tubes: 'les tubules paraissent véritablement creux'). Most of the papillae which I examined are broken, having lost their thin outer walls. They appear as long (much longer than the intact papillae) white threads, some having small pigmented tips.

In the specimens of *Saccopharynx* the papillae are less transparent and their apexes are wider, but their structure is apparently the same as in *Eurypharynx*. The whitish discs on the skin at the bases of the papillae are more distinct, and connected with each other, along the main lateral line of the body, by a thin white line (first shown in *Saccopharynx* by Girard, 1895).

These papillae of Lyomeri are very similar to those described by Regan and Trewavas (1932, pp. 23, 24) in *Photocorynus* (Ceratioidea). After a study of sections of the skin and of lateral-line papillae, these writers came to the conclusion that the white apex of the papilla is a sense organ 'exposed and raised above the surface of the body', and the white thread inside the papilla is a nerve. According to these writers, in Ceratioidea 'glandular cells may be present in the papilla, which is formed mainly of loose fibrous tissue'. They write also that 'a tube that may represent the lateral line canal may be present between the papillae, or may be replaced by a superficial groove, either continuous or discontinuous'. In *Photocorynus* the white discs at the bases of the papillae along the lateral line are connected by a white line, as in *Saccopharynx*.

In *Cyema* (in which the sensory system papillae are like those of Lyomeri) the posterior part of the infraorbital canal (extending over the sphenotic and the pterotic) is well ossified, and forms the dermal part of the pterotic (which corresponds apparently to the 'supratemporo-intertemporale' of Holmgren and Stensio). In Lyomeri the dermal pterotic has also the features of a sensory canal bone.

It seems, therefore, reasonable to suppose that in Lyomeri, as in other fishes, the disposition of the lateral line system may be considered as a guide to the homology of some of their cover bones.

The disposition of the sensory canal system in Lyomeri.—Bertin (1934, pp. 13, 15, 49, 50), who had for study the magnificent material of the 'Dana' Expedition (63 adult and 123 young), described the disposition of the lines of this system in Lyomeri. Unfortunately, he does not mention the relation of this system to the elements of the skeleton, does not compare the disposition of the lines of this system in Lyomeri with that found in other fishes, and uses a nomenclature of his own for the sensory canal series.

Comparing his figures with the figures of earlier writers on Lyomeri (Brauer, 1906; Zugmayer, 1911) and with the specimens in the British Museum, one can describe thus the disposition of the sensory system on the head of *Eurypharynx*.

The supraorbital series.—A series of single papillae extends on each side from the anterior dorsal part of the rostrum where the nasal bone is situated (Pl. 8, fig. 1, *N*.) and continues dorsally, round the orbit following the ridge of the frontal, then turns outwards just behind the eye, where it comes very close to the infraorbital canal, and possibly joins with it. According to the terminology of Bertin the supraorbital series is the anterior part of the 'rangée I'. This series can be more or less distinctly followed on the specimens in the British Museum.

It is rather clear that in *Eurypharynx* the supraorbital canal is connected with the nasals and the ridges of the frontals.

The ethmoid commissure.—A series of apparently eight papillae extends across the dorsal side of the ethmoid region between the two nasal bones. This is rather distinct in one of the specimens of the British Museum. Bertin does not show this series.

The infraorbital series.—The course of the infraorbital series is unusual. The main series of papillae (in groups of four or five alternating with single papillae) runs along the edge of the bone forming the upper jaw. Zugmayer (1911, pl. iv, fig. 3, p. 92) shows it very distinctly and describes it as a series disposed along the edge of the upper jaw. The series arises on the ventral side of the head under the eye, where the two rami of the upper jaw articulate; then extends backwards close to the edge of the mouth and terminates before reaching the hind end of the jaw. In the young specimen of *Eurypharynx* (p. 301) it extends for about three quarters of the length of the upper jaw (Bertin calls it 'rangée VI').

Several (four or five) papillae, apparently of this series, are found on the ventral side of the head in front of the eye, and three papillae form a branch ascending behind the eye to the upper hind edge of the orbit where the sphenotic is situated (Pl. 3, fig. 1, *S.*). From this point this branch turns sharply backwards along the edge of the sphenotic and pterotic (single papillae), where it comes very close to the supraorbital canal.

Lateral line of the body.—Behind the cranium a series (single papillae alternating with groups of papillae) extends along the dorso-lateral side of the body to the end of the tail forming the *lateral line* of the body ('rangée II' in Bertin's figure). As the supraorbital and the infraorbital series lie very close together, it is difficult to say which of these series is prolonged into the main lateral line series.

Quadrato-jugal or preopercular series.—A series of single papillae runs along the suspensorium from somewhere near the eye (its anterior extension is not clear) to the articulation of the suspensorium with the lower jaw (Bertin calls this series 'rangée V'). It may correspond to the proximal part of the preoperculo-mandibular line or to the quadrate-jugal pit line or the vertical pit line of the cheek of Osteolepis. In the adult fish this series lies close to the infraorbital series, following the edge of the mouth dorso-posteriorly to the infraorbital series; in the larva it extends along the dorso-posterior edge of the suspensorium.

Occipital commissure.—A series of single papillae extends from the hind edge of each pterotic obliquely backwards and towards the mid-dorsal line, but terminates before reaching this line, so that it does not meet its fellow.

Beside the occipital commissure, two more rather irregular series of papillae can be distinguished: one along the dorsal side of the pterotic, and the other disposed more or less across the skull in the region of the parietals. None of these series is shown by Bertin, though it is possible that one of them corresponds to the oblique series of papillae behind the eye, which Bertin calls 'seconde boucle' of the 'rangée I'.

Finally, there are two more series of single organs the homology of which is not clear. One extends from the hind edge of the pterotic (the skin in the specimen examined is broken, and the origin of this series is not visible) and extends backwards between the suspensorium and the vertebral column, and then along the upper edge of the branchial aperture. It terminates just in front of the pectoral fin. This series corresponds to Bertin's 'rangée IV'.

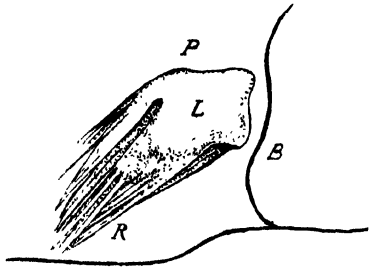
The other series extends along the middle ridge of the back from just behind the cranium to the anterior end of the dorsal fin (Bertin's 'rangée III'). The latter series has no connection with the skeleton, and from Bertin's (1934, p. 50, fig. 44) description and figure this series is completely absent in *Saccopharynx*.

It is perhaps important to stress that in Lyomeri no series of sense organs along the lower jaw is found. Brauer (1906) and Zugmayer (1911) do not show any such series on their careful coloured plates, and Zugmayer (1911, p. 92) describing the sensory canal system of *Eurypharynx* does not mention this series; neither does Bertin (1934) show it in his diagrams or mention it in the description either of *Eurypharynx* or of *Saccopharynx*. Unfortunately, in the adult specimens examined the skin of the lower jaw is completely missing, and the absence of this series could not be verified. I could find no trace of it in the young *Eurypharynx* (p. 301).

Summary.—Little is known about the sensory canal system of Lyomeri. From an external incomplete examination series of papillae corresponding to the supraorbital and infraorbital canals can be distinguished. The supraorbital series extend over the nasals and the frontals. The largest and most important part of the infra-

orbital canal (consisting of groups of papillae) follows closely the edge of the bone forming the upper jaw ; a branch of apparently the same series, extends along the edge of the sphenotic and pterotic, and consists of single papillae. There are two series running from the posterior edge of the orbit backwards ; one along the suspensorium, the other dorsally to it, across the cheek to the branchial region. There is no lateral line along the mandible. The main lateral line of the body originates near the posterior edge of the orbit where the supraorbital, infraorbital and the two series running along the suspensorium and dorsally to it all join very close together. It is not clear from which of these series the main lateral line arises.

Dermal bones connected with the lateral line system.—In *Eurypharynx* the bones connected with the sensory canal and pit liniae systems, the nasals, frontals, parietals, dermal pterotics, can be distinguished. There is possibly also a dermal sphenotic (p. 319). There are no separate orbital series of bones, but it seems possible that the infraorbitals are fused with the anterior end of the upper jaw. There is no preoperculum ; the structure of the lower jaw does not suggest any connection between its bones by a sensory canal.

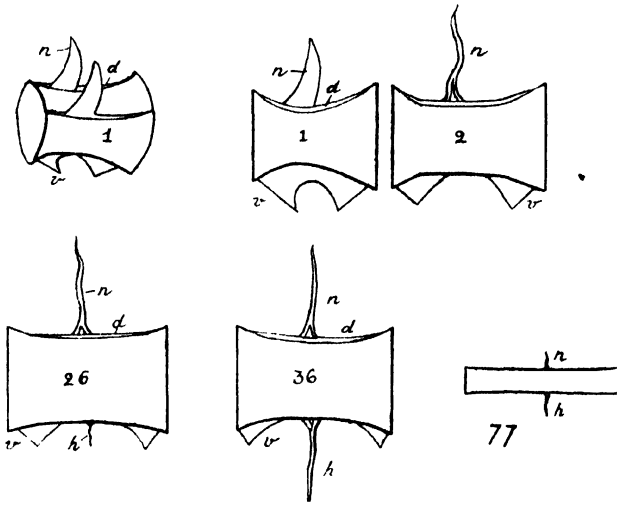


TEXT-FIG. 9.—Pectoral fin of *Eurypharynx pelicanoides*. Right side. About × 15. Diagrammatic. *B.*, posterior end of the branchial fold ; *L.*, lobe of the pectoral fin ; *P.*, pectoral fin ; *R.*, fin-rays.

(d) *The skeletons of the pectoral girdle, of the vertebral column, and of unpaired fins.*—*Shoulder girdle and skeleton of pectoral fins* (text-fig. 9).—The pectoral fins of Lyomeri are supported by fleshy peduncles markedly projecting beyond the sides of the body. Their skeletons and the skeleton of the pectoral girdle have never been described. Unfortunately, the clarified specimen of *Eurypharynx* which I studied has the branchial and pectoral parts in poor condition. It is clear however, in this specimen that the pectoral fins have lobate basal parts, and that the left and right pieces of the shoulder girdle are probably disconnected. More details of these structures are given in the description of *Saccopharynx* (p. 335) *.

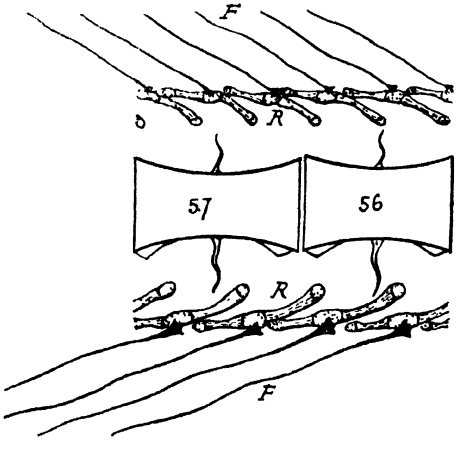
The vertebral column (text-figs. 10, 11). Nussbaum-Hilarowicz (1923, pp. 58–60, pl. viii, figs. 3–5, 12–16) has studied the structure of the vertebral column of *Eurypharynx* in prepared sections. The main points of his study can be thus summarized. The notochord is persistent in adult specimens and only surrounded by osseous cylinders representing the centra of vertebrae. The notochord extends, apparently without any interruption, from the base of the cranium to the tip of the tail. The tissue of the notochord consists of vacuolated cells. A canal, or an oblong cavity, is found at the centre of the chorda between its cells ; and extends through the whole length of the notochord. The elastica chordae, homogenous in structure, is rather thick, and also persists through the whole length of the notochord. No epithelium of the notochord was found. The outer shell of the vertebrae is formed by bony

* See Tchernavin 1946 a.



TEXT-FIG. 10. -Vertebrae of *Eurypharynx pelicanoides*. Diagrammatic. × about 15. Upper figure on the left shows the first vertebra seen from the left side and from above, the next figures show the 1st, 2nd, 26th, 36th and 77th vertebrae from the left side. The numbers show the ordinal number of the vertebrae.

d., dorsal ridge of the vertebra, *n*, dorsal process (neuropophysis); *h.*, ventral process (haemapophysis), *v*, ventral ridges.



TEXT-FIG. 11.—56th and 57th vertebrae of *Eurypharynx pelicanoides* and the skeleton of the unpaired fins of their region. Right side × about 15. Diagrammatic.

F., fin-rays; *R.*, radials.

tissue with elongated cells. In the basal part of each neurapophysis and haemapophysis a small hyaline cartilage is found. This cartilage is enveloped by a homogeneous bony tissue (*loc. cit.* p. 59, pl. viii, fig. 16).

According to Nussbaum-Hilarowicz, in the posterior part of the tail the vertebral column is very much reduced, and formed by a continuous long tubule with a central cavity which is continuous with the central canal of the notochord (pl. viii, fig. 13).

From the morphological point of view the vertebrae in the small specimen I studied can thus be described. The bodies of the vertebrae, except those in the posterior part of the tail, have the shape of cylinders only slightly narrowing in the middle (hour-glass shaped). Their long shells are very thin and easily deformed in preservation. They have paired longitudinal dorsal and ventral ridges and paired processes, the latter probably representing the neural and haemal processes. These ridges and processes are differently developed in different vertebrae. The tips of the paired processes diverge and never meet their fellows of the other side. Thus the neural canal has no bony supports from above, and the haemal canal has no bony supports from beneath. As these processes are very narrow, the walls of both canals are mostly membraneous. There are no neural, nor haemal spines.

The first vertebra (text-fig. 10) is only slightly longer than deep. A pair of lamelliform longitudinal ridges extend along its dorsal side (*d.*). Slightly in front of the middle of the vertebra a pair of dorsal processes (*n.*) arise. These processes are thin and triangular; laterally they are confluent with the dorsal ridges. These processes, possibly together with the dorsal ridges, represent the neuropophyses. The tips of these processes (on the left and right side) are widely separated from one another. A pair of longitudinal thin ridges or lamellae (*v.*) extend along the ventral side of the vertebra, they are deeper at the ends of the vertebra and lower at its middle. These ventral lamellae bear no processes corresponding to those of the dorsal side.

The second vertebra (text-fig. 10) is noticeably longer than the first, and as deep as the first vertebra at its posterior end. It has dorsal ridges (*d.*) similar to those of the first vertebra, but its dorsal processes (*n.*) are much narrower, rod-like, narrowing into a thread at their tips. In the clarified specimen which I studied, the base of each of these processes appears double, with a triangular space, not stained with alizarin, between the roots of the process. These triangular spaces correspond probably to the cartilage enclosed between the roots of the processes, as described by Nussbaum-Hilarowicz (1923, pl. viii, fig. 16). The ventral ridges on each side are interrupted in the middle, each ridge forming two separated triangular lamellae (*v.*).

The next 23 vertebrae are in size and structure similar to the second vertebra, varying only slightly in the development of the dorsal processes and ventral ridges.

The 26th vertebra (text-fig. 10), which is approximately opposite the anus, differs from those in front of it by having smaller and more widely separated ventral triangular lamellae (*v.*), and by having a pair of small ventral processes (*h.*) corresponding in position to the dorsal processes (*n.*); they are probably the haemapophyses. In the three next vertebrae these ventral processes become gradually longer and attain the size of the dorsal processes, and even become longer than the dorsal processes in the vertebrae situated posteriorly. The shape and structure of these ventral processes are extremely like those of the dorsal processes described in the second vertebra. Such a vertebra, the 36th, is shown in text-fig. 10.

At about the 50th vertebra (text-fig. 11) the vertebrae become gradually less deep, their dorsal and ventral ridges less developed and the processes smaller. The 77th vertebra (shown on text-fig. 10) is of the same length as the second vertebra, but its diameter is about three and a half times as small. Its ossified shell is very thin. At about the 90th vertebra the alizarin has hardly at all stained the shells

of the vertebrae, and it seems doubtful whether there is any ossification whatever round the notochord at the posterior part of the tail. Only very indistinct subdivisions of the vertebral column could be seen in this region. Including them the numbers of vertebrae in this specimen is estimated as 106. The vertebral column ends posteriorly with a thin and small threadlike projection, which is not turned upwards. No hypurals could be seen in the specimen studied by me.

According to Nussbaum-Hilarowicz (p. 60, pl. viii, figs. 12, 13), sections through the tip of the tail in the region of the caudal organ show that there is a rather large cartilage compressed from side to side. This cartilage is completely separated from the vertebral column and forms the axis of the swollen part of the tail; it lies dorsally to the vertebral column.

Bertin (1934, fig. 7) shows the posterior end of the vertebral column consisting of rather stout and short well-formed vertebrae, ending in a long process forked posteriorly. The upper branch of this fork he styles as urostile, and the lower branch as hypural. This figure disagrees, however, with Bertin's own description of this structure on p. 20 of the same paper.

Ribs, epineurals, epicentrals and pleurocentrals are absent.

Skeleton of the unpaired fins (text-fig 11).—The skeleton of the unpaired fins in *Eurypharynx* was described by Gill and Ryder (1883), Nussbaum-Hilarowicz (1923), and Bertin (1934); the latter writer showed the structure of these elements in figures.

In the small specimen which I studied, the skeleton of the unpaired fins is thus formed. The fin-rays (*F.*) are tender and flexible, each fin-ray consisting of a pair of rays (right and left) which are not fused together (compare Bertin, 1934, fig. 16). The proximal ends of the rays are broadened and denticulated, forming projections for muscular attachment. The distal ends of the rays are filament-like. In the specimen clarified and stained with alizarin the rays are coloured bright red. This suggests that they are well ossified. Under a microscope the rays appear of homogeneous structure; no bone-cells could be seen, the rays are unbranched and unjointed (not segmented), no trace of lepidotrichia are visible. All fin-rays of the dorsal and anal fins have the same structure, and differ only in size.

How can these rays be compared with the fin-rays of other fishes? They are apparently well ossified but have no sign of transverse divisions, and thus cannot be regarded as lepidotrichia. Being soft, flexible and unsegmented they recall the ceratotrichia, but are bony, while the main characteristic of ceratotrichia is that they 'never become ossified' (Goodrich, 1904, p. 469).

The radial elements of the dorsal and anal fins differ in size but not in structure. Each fin-ray is supported by a single, compound, radial element. A radial element consists of two segments united by a cartilage. The proximal segment (corresponding to the first radial) originates medially at some distance from the vertebra and extends obliquely backwards and towards the surface of the body; the distal segment (corresponding apparently to the second radial) extends backwards along the outer edge of the body (on the ventral and dorsal sides). Each of the segments has an externally ossified shaft; the portion between the segments is cartilaginous. I could not see any division in this portion. The proximal and distal ends of the radial (consisting of two segments) are cartilaginous. The proximal ends of the radials are not attached to the neuropophyses, or haemapophyses. The distal end of each radial is attached by a ligament to the cartilaginous middle portion of the next radial. I could not find a third radial segment, or a third radial, described and figured by Bertin (1934, p. 20, fig. 16).

In the specimen which I studied many rays and their radials are missing in the anterior part of the body, and I could not examine their relation to the vertebral column all along its length. In the part of the body which was in sufficiently good

condition the anal fin-rays are metamerically disposed, two rays corresponding to one vertebra. But the dorsal rays are more numerous, and their disposition does not well agree with the vertebrae. For instance, between the 47th and 56th vertebrae (10 vertebrae) I counted 19 anal and 26 dorsal fin-rays. (Compare Bertin, 1934, p. 20, figs. 13, 14, 15, 19.)

3. *The Skeleton of* Saccopharynx.

Little is known about the skeleton of *Saccopharynx*. Some remarks on it are to be found in Günther's (1887) and Girard's (1895) descriptions of this fish. Regan (1912 *a*) gave a primitive diagram of the dorsal view of the cranium of *Saccopharynx*. Bertin (1934, pp. 39, 40, fig. 34) apparently copied this diagram with a few alterations and gave an original figure (fig. 35) of the jaws and the suspensorium of *Saccopharynx*. The latter figure does not show the structure of the elements concerned, nor give an accurate idea of their mutual disposition. Bertin's description of the skull of *Saccopharynx* deals mostly with the dimensions of its parts but not with their structure.

(a) *The skull.*—The main peculiarities of the head and the skull of *Saccopharynx* are given on p. 302. The structure of the head is in general similar to that of *Eurypharynx*, but differs substantially in detail. The *Saccopharynx* has five visceral clefts and four gills. The vomer and parasphenoid are absent. The *mm. obliqui* of the eye arise from cartilages separate from the chondrocranium. The ethmoid region is narrow and long and covered by a membrane bone.

The most important difference in the structure of the head of *Saccopharynx* from that of *Eurypharynx* is the differently built branchial apparatus, and a few words must be said on this structure before its skeleton is described.

The branchial apparatus of Saccopharynx can thus be briefly described :—

The branchial clefts are of unusual shape (Pl. 2, fig. 2) ; they are horizontally (not vertically) elongated holes, not compressed from side to side, as usually in fishes. The septa between the clefts are rounded, fleshy bars ; they are widely separated from each other by the broad clefts. There are no gill-rakers. A muscular band extends along the dorsal edge of the visceral clefts, a similar band extends along their ventral edge. These two muscular bands meet each other in front of the anterior visceral cleft, and behind the last one, surrounding thus the five visceral clefts and forming a kind of muscular sphincter. The septa between the clefts are attached dorsally and ventrally to these muscular bands. According to Günther (1887, p. 259) the septa between the clefts are supported by cartilaginous rods and thus correspond to the visceral arches or rather to semi-arches, for those of the left and right side of the body do not meet each other ventrally, and are separated by the ventral wall of the body, which is very extensible. There are no basal skeletal elements uniting the semi-arches of the left and right sides.

Owing to such a structure the visceral septa look like narrow bridges arching over a single long horizontal slit.

The anterior cleft is much compressed dorso-ventrally, and is not visible unless the branchial apparatus is extended (as shown in Pl. 2, fig. 2). The first septum is knee-shaped with its apex directed forwards. The second cleft is much longer and deeper ; the septum behind it is nearly straight ; the third cleft is about as long as deep, and the septum behind it is similar to the second septum. The fourth cleft is the largest, about three times as long as deep ; the fourth septum is knee-shaped, with its apex turned backwards.

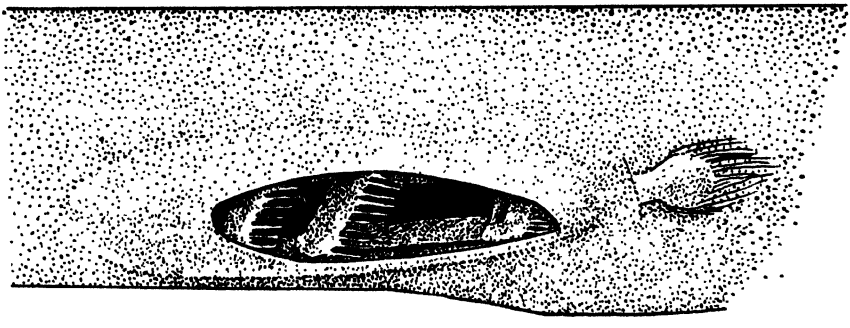
The dorsal and ventral muscular bands extended along the visceral clefts join together behind the fourth septum, and the wall of the pharynx is not perforated behind this septum, which bridges over the pharyngeal wall, where an indistinct fold is formed. The significance of this fold is not clear.

At some distance behind the fourth septum there is another sack-shaped fold, which possibly is a rudiment of the fifth septum and arch (Pl. 2, fig. 2).

All five clefts are surrounded from the outside by a fold of integuments (text-fig. 12). This fold is longer anteriorly and dorsally than posteriorly and ventrally It forms (on each side) a kind of imperfect branchial chamber, with an aperture, which cannot be closed and through which parts of the second, third and fourth arches are visible. This fold is not supported by bones.

I could see only one hemibranch on each of the four septa. The specimen which I examined is in poor condition and I could not count the branchial filaments nor study their structure.

The visceral skeleton.—The general structure of the suspensorium and jaws of *Saccopharynx* is similar to that of *Eurypharynx* (text-figs 4, 5). They differ, however, in proportion and in some details. The jaws and the suspensorium are shorter, the mandible being nearly three times as long as the cranium When the mouth is



TEXT-FIG. 12.—Left branchial chamber and the pectoral fin of *Saccopharynx ampullaceus* Through the branchial aperture the first, second and third branchial arches can be seen. Branchial clefts black. Semi-diagrammatic. 3.

shut and the posterior end of the suspensorium is directed down and backwards, the mandibulo-quadrate articulation lies on the vertical line of the tenth vertebra. The elements of the jaws and of the suspensorium are heavier built than in *Eurypharynx* and the jaws bear large, curved teeth.

The hyomandibular (text-fig. 13, *H.*) articulates with the cranium by a single condyle received into a deep socket on the ventral side of the cranium. The shaft of the hyomandibular is subcylindric, only partly ossified, mainly along its surface. The distal end of the hyomandibular is cartilaginous, and apparently articulates by harmony with the exactly similar proximal end of the quadrate. The method of this articulation is obscured in the specimen which I studied by the attempts of earlier investigators to prove that the quadrate ' is capable of being swung in all directions '; the cartilage and all bones in this part of the suspensorium are broken.

A strong and well-ossified lamella (*l.*) extends medially from the proximal end of the hyomandibular, along its shaft and further down to about half the length of the quadrate. This lamella is firmly and immovably attached to the inner side of the shaft of the hyomandibular along its whole length and also to a large part of

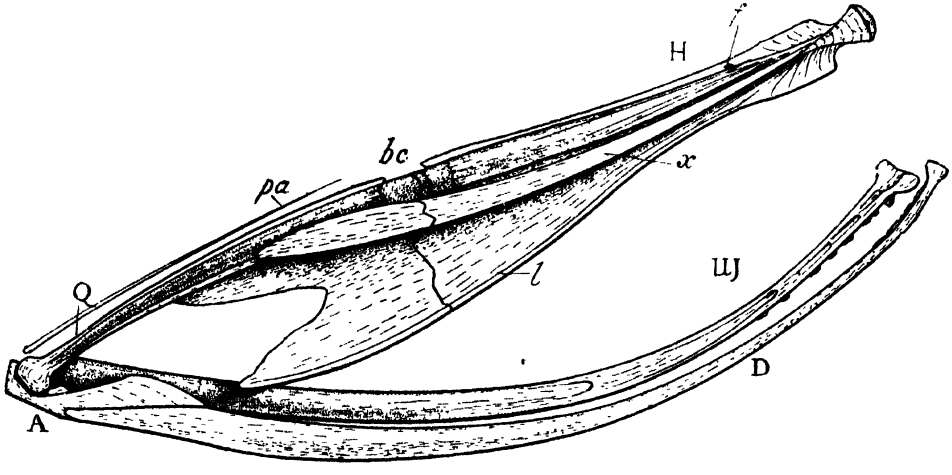
the quadrate. The main body of this lamella is triangular-shaped with its apex lying closely under the articulating condyle of the hyomandibular. The large *m. adductor mandibulae* arises partly from this lamella.

Close to the articulating condule of the hyomandibular and posteriorly to the main rod of this bone, it is perforated by a nerve, which presumably is either the *truncus hyomandibularis* vii, or the *n. mandibularis internus*.

A rod-like ossification (*x*.) lies laterally to the hyomandibular and extends along the quadrate. Its proximal end is very thin and firmly attached to (apparently fused with) the proximal part of the hyomandibular; its distal end is attached to the quadrate. I find no grounds for judgment whether this rod is a second limb of the hyomandibular or not.

Both the medial lamella of the hyomandibular (*l*.) and the well ossified rod-like element (*x*.) extend over the hyomandibulo-quadrate articulation and both are firmly united with the hyomandibular and the quadrate. This makes the movements of the hyomandibulo-quadrate articulation impossible.

There is no *processus opercularis*.



TEXT-FIG. 13.—Suspensorium mandibulae and the jaws of *Saccopharynx ampullaceus*. Diagrammatic. Enlarged. The teeth are lost in the specimen from which the figure is made and are not shown in the figure. The suspensorium in this specimen is broken in the region where the quadrate joins the hyomandibular.

A., the posterior bone of the lower jaw; *D*., the anterior bone of the upper jaw; *H*., hyomandibular; *Q*., quadrate; *U.J*., upper jaw bone; *bc*., cartilaginous epiphyses of the quadrate and hyomandibular (broken in the specimen figured). *f*., foramen for the *r. mandibularis internus* of the facial nerve; *l*., lamella of the hyomandibular; *pa*., ossified tendon of the *m. abductor mandibulae*; *x*., bone co-ossified with the hyomandibular and the quadrate (metapterygoid ?, second limb of the hyomandibular ?).

The quadrate is a long rod similar to the main rod of the hyomandibular. Its end articulating with the hyomandibular is cartilaginous but ossified on the surface; its lower end is well ossified and forms a double rotatory diarthrosis for articulating with the mandible. The quadrate is strengthened by two narrow lamellae which extend along its posterio-dorsal and anterio-ventral surfaces. These lamellae are apparently fused with the lamella of the hyomandibular (in the specimen which I studied they are broken).

The mandible consists of three parts which can be readily distinguished: the very long, curved and rod-like anterior part (*D.*) which bears teeth and corresponds in position to the dentary; the short posterior part (*A.*), which articulates with the quadrate and serves for the insertion of the *m. adductor mandibulae*: the third part is Meckel's cartilage. The rod-like anterior part bears teeth on its inner surface, it extends from the tip of the mandible to near the mandibulo-quadrate articulation. The anterior $\frac{7}{8}$ of this bone are tubular, closed all round, and only the posterior $\frac{1}{8}$ becomes boat-shaped and hold Meckel's cartilage from beneath, and partly ensheaths it. The posterior end of the mandible extends posteriorly beyond the articulation with the quadrate, where a strong tendon of the muscle *abductor mandibulae* inserts into the posterior end of the mandible. This tendon is partly ossified, forming a long narrow bone (*p.a.*) lying behind and parallel to the quadrate. The posterior bone of the mandible is apparently a compound bone, but there is no evidence for a judgment on the homology of its parts. There is no sign of connection of the bones forming the mandible with the lateral line system.

The *m. adductor mandibulae* inserts by several ligaments to the inner surface of the posterior bone of the mandible in front of the articulation of the latter with the quadrate. This muscle has no part extending along the mandible itself.

The two rami of the mandible articulate movably in the mental symphysis, this articulation is not loose.

The upper jaw (*U.J.*). The general shape and structure and the relation to the cranium and the suspensorium of the upper jaw of *Saccopharynx* are similar to those of *Eurypharynx* (p. 311), but the bone is heavier and its structure is more evident. Its anterior part bears teeth on the medial, inner surface of the bone. The teeth are movable and set in sockets; the bony substance round each socket is thickened. Along the outer (lateral) side of the anterior part of this bone there are indistinct traces of a canal enclosed in the bone, similar to those found in the dentary of teleosts. As the infraorbital branch of the lateral line system extends over this part of the upper jaw, there is reason to suppose that the lateral anterior part of the upper jaw may correspond to the suborbitals.

The posterior part of this bone is much heavier and its hind end is compressed from side to side. This part of the bone consists of a cartilage-like tissue and is ossified round its surface only. The two rami of the upper jaw articulate under the cranium in the region of the eyes. The tips of the rami are attached by a strong ligament to the cranium (text-figs. 4, 5, *L.*).

The posterior end of the upper jaw lies medially to the triangular lamella of the hyomandibular, to the quadrate and to the mandible. It is attached by a strong ligament to the medial surface of the quadrate, close to the articulation of the latter with the mandible. Thus the mandibulo-quadrate articulation lies laterally to the upper jaw. The *m. adductor mandibulae* is also situated laterally to the upper jaw. This muscle has a separate portion which inserts laterally into the hind end of the upper jaw by means of a long ligament.

The medial position of the upper jaw, its relation to the hyomandibular, quadrate, mandible, to the *m. adductor mandibulae*, and to the infraorbital branch of the lateral line system suggests that a part of it corresponds to the palatine, and that the suborbitals may have taken part in the formation of its anterior lateral edge.

According to Regan (1912 *a*, p. 348), the upper jaw of *Saccopharynx* is the 'praemaxillo-maxillary', and the mandible is formed by the dentary, articulare and angulare. According to Bertin (1934, pp. 4, 7, 40, fig. 35), both jaws of *Saccopharynx* are in a state of cartilage, the upper jaw being a 'maxillaire'.

The structure of the suspensorium and of the upper jaw are so similar to those of *Eurypharynx* that there can be no doubt that the elements concerned are homologous in both fishes. There are also no ventral hyoid elements attached to the

suspensorium mandibulae and there is no trace of opercular series (operculum, suboperculum and interoperculum absent); there is no preopercle, and no branchiostegals. (Regan's statement, 1912 *a*, p. 348), that the branchiostegals are vestigial, is not correct.)

Less clear is the homology of the visceral elements and arches supporting the septa of these clefts. The presence of the fold behind the fourth septum, and the fact that the cleft behind the fourth septum is almost entirely closed, suggest that the posterior part of the branchial apparatus of *Saccopharynx* is reduced and that the posterior branchial cleft was lost.

It seems thus that the anterior visceral cleft and holobranch in *Saccopharynx* are homologous with those of *Eurpharynx*; their nature is not clear, and can be established only by the study of the relations of the cephalic nerves to the visceral arches. Unfortunately these nerves are completely torn off in the specimen of *Saccopharynx* which I have in hand.

The branchial skeleton of *Saccopharynx* has not attracted the attention of earlier writers. Günther (1887, p. 259) describes five branchial arches in *Saccopharynx* and their skeleton as 'extremely slender, merely thin cartilaginous rods with an indistinct knee-shaped bend'; Regan (1912 *a*, p. 348) does not mention the number of arches, but says that these arches are 'little ossified'. It must be noticed that Günther and Regan described the same specimen; Bertin, 1934, in his monograph on Lyomeri does not mention at all the branchial skeleton of *Saccopharynx*

The Neurocranium (Pl. 3, figs. 3, 4).—The chondrocranium is largely unossified and its parts are movably articulated. Two dorsal processes of the basioccipital articulate movably with the lateral occipitals, and the processes of the prootics articulate movably with the processes of the sphenotics. The structure of the roof of the chondrocranium covered for the greater part with bones has not been studied. It is clear, however, that the primordial cartilage of this roof has no division corresponding to the supraoccipital. Two cartilages, separate from the chondrocranium, are situated at the anterior edge of the orbit, and serve for the attachment of the *mm. obliqui* of the eyes. These cartilages correspond possibly to the lateral ethmoids; they are absent in *Eurypharynx*.

The neurocranium has not been dissected nor clarified; thus the extension of the cranial cavity and the structure of the auditory organs are not known. It seems clear, however, that the brain case extends anteriorly above the orbital region. The position of the optical and olfactory nerves could not be examined in the mutilated specimen which I studied. There are no grooves in the skull for lodging the olfactory organs. The interorbital cartilage is low (no proper interorbital septum), and there is no myodome.

The occipital region (Pl. 3, figs. 3, 4) consists of the same three elements as in *Eurypharynx*; the basioccipital and the two lateral occipitals. There is no supraoccipital. The oblique position of the *foramen magnum* is similar to that of *Eurypharynx*. The *n. vagus*, and apparently the *n. glossopharyngeus*, pass through a foramen between the basioccipital and the lateral occipital. The lateral occipital has a depression for the passage of this nerve, or nerves (Pl. 3, fig. 4). In *Eurypharynx* the foramen for the nerves of the vagus group perforates the lateral occipital (Pl. 3, figs. 1, 2).

The articulating surface of the basioccipital is deeply concave, funnel-shaped. The anterior end of the notochord persists through at least half the length of the basioccipital. Bertin calls the concave articulating facet of the basioccipital: 'l'unique condyle d'articulation avec la première vertèbre'; however, no condyle was found in the specimen which I studied.

The absence of the supraoccipital (Pl. 3, fig. 3) is most clear. The two lateral

occipitals unite by harmony above the *foramen magnum*, and leave no space for the supraoccipital; there are no medial ossifications or divisions in the primordial cartilage of the chondrocranium in front of the *foramen magnum*. In a little sketch of the *Saccopharynx* skull, Dr Regan (1912 *a*, p. 348, fig. B) shows a very small spot dividing the two lateral occipitals above the *foramen magnum*, he calls it the supraoccipital. I examined very carefully under a microscope the skull of the same specimen of *Saccopharynx* which Dr. Regan described and figured (the only one dissected in the British Museum) and could not find any trace of the supraoccipital. Bertin (1934, p. 39, fig. 34) describes the supraoccipital of *Saccopharynx* as 'très petit', but does not show it in his figure, and does not mention it in the legend to his figure, where all other bones are referred to.

There is no supraoccipital in Lyomeri.

The basioccipital (*B*.) (Pl. 3, figs. 3, 4) is a large and well ossified bone. As in *Eurypharynx*, a large part of this bone extends posteriorly beyond the edge of the *foramen magnum* and has very much the structure of a vertebra. It is shaped as a hollow cylinder containing the notochord, and has two pairs of processes, a dorsal and a ventral pair, corresponding to the neural and haemal processes of a vertebra. The dorsal processes (Pl. 3, fig. 3, *BD*.) form part of the walls of the neural canal, the ventral processes (Pl. 3, fig. 4, *BV*.) play the role of the haemal arches in serving for the insertment of the lateral muscles of the body. In the groove between these processes the medial dorsal aorta is possibly lodged. But I could not verify it in the mutilated specimen which I studied. It can be mentioned here that, according to Nussbaum-Hilarowicz (1923, p. 70), there is probably a pair of cerebrospinal nerves between the myelencephalon and neural cord in *Eurypharynx*.

The dorsal processes of the basioccipital (*BD*.) are short and stout cylinders articulating with the lower ends of the lateral occipitals. The articulating surfaces of these processes and of the lateral occipitals are deeply concave, and enclose between them a globular piece of gelatinous tissue. This articulation is clearly a movable one. The ventral processes of the basioccipital (*BV*.) are stout and long. The proximal parts of these processes are well ossified, their distal parts consist of cartilage. In Pl. 3, fig. 4, the cartilagenous part of the left process is removed to show the structure of the ossified part. The lateral muscles of the body are inserted into the cartilage of this process and serve for depressing the cranium.

The ventral anterior part of the basioccipital of *Saccopharynx* is markedly shorter and broader than in *Eurypharynx*.

The basioccipital articulates ventrally with the prootics by synchondrosis; this articulation is movable owing to the elasticity of the intermediate cartilage.

The lateral occipitals.—The position and shape of the lateral occipitals are shown in Pl. 3, figs. 3, 4. Dorsally they articulate by synchondrosis with the epiotics and cartilage pterotics, ventrally and posteriorly with the cartilage pterotics. The foramen (*f*.) for the nerve of the *vagus* group separates them ventrally from the basioccipital and permits a greater mobility to their dorsal articulation with the latter bone.

The otic region (Pl. 3, figs. 3, 4) consists of the same five pairs of cartilage-bones as in *Eurypharynx*; the pterotics (fused with their dermal pterotics) (*PT*.); the epiotics (*E*.), the sphenotics (*S*.), and the prootics (*P*.). There are no opithotics, no alisphenoids and no basisphenoid.

The pterotics (*PT*.) (Pl. 3, figs. 3, 4).—Each pterotic consists of two parts fused together; the cartilage-pterotic (the name is used here as by de Beer, 1937, pp. 127 132, 139, 160, and is equivalent to the 'opisthoticum' of Holmgren and Stensio 1936, pp. 490, 494, fig. 373), and the dermal part, the intertemporal, or the derma

pterotic. The cartilage-pterotic extends posteriorly beyond the dermal part. It can be seen that ventrally the narrow dermal ossification of the pterotic extends over the sphenotic and is fused with the latter. Dorsally the dermal pterotic expands broadly over the side of the cranium. The relation of this part of the pterotic to the cartilage is not clear, but it apparently encloses a part of the infraorbital sensory canal. It appears that the dermal pterotic of *Saccopharynx* corresponds to the inter-temporal post-temporal In *Eurypharynx* these parts of the dermal pterotic and sphenotic are separate.

The skeletal element between the lateral occipital and the pterotic which Regan (1912 *a*, p. 348, fig. A) figured and described as 'epiotic', and Bertin (1934, p. 39, fig. 34) called 'opisthotic', does not exist (see also p. 318).

The sphenotics (*S.*) (Pl. 3, figs. 3, 4) are large and well ossified. Dorsally the sphenotic appears as a long narrow bone extending along the outer edge of the frontal. Ventrally and anteriorly it forms the posterior edge of the orbit, and ventrally and posteriorly it forms the anterior part of the articulating groove for the condyle of the hyomandibular. Inside this articulating groove the sphenotic is separated from the pterotic and from the prootic by broad cartilage-bridges. The sphenotic sends out ventrally and medially a strong process for articulation with a similar process of the prootic. The articulation surfaces of both these processes are of cartilage and the articulation is a mobile one. From the sculpture of this bone it seems probable that its outer edge, fused with the dermal pterotic and forming its anterior extension, is a dermal bone related to the infra-orbital canal.

The epiotics (*E.*) (Pl. 3, fig. 3) of *Saccopharynx* do not extend as far forwards as in *Eurypharynx*. Anteriorly they almost reach the hinder edge of the frontals. There are no separate parietals in *Saccopharynx*.

According to Regan (1912 *a*) and Bertin (1934), the bones described here as epiotics are 'parietals'. The 'epiotic' of Regan (= 'opisthotic' Bertin) corresponds to the lateral part of the lateral occipital, the posterior part of the cartilage-pterotic, and to the cartilage dividing these bones. When the skull is examined dorsally, and is not properly cleaned, these elements protruding slightly backwards may be taken for a separate bone.

The prootics (*P.*) (Pl. 3, fig. 4) are disposed more posteriorly than in *Eurypharynx*, which corresponds to a more posterior position of the epiotics. Contrary to what is found in *Eurypharynx*, the prootics do not project medially into the interorbital region. The ventro-lateral processes of the prootics, articulating with the ventral processes of the sphenotics, are very strong. The prootics of the left and right sides are divided by a narrow strip of the cartilage of the cranial floor. The relations of the prootics to the *m. trigeminus* and *facialis* are similar to those found in *Eurypharynx*.

Regan (1912 *a*) does not mention the prootics in *Saccopharynx*; the bones described here as the prootics are not the 'prootics' of Bertin (1934, p. 39, fig. 34), which are the dermal parts of the pterotics.

The orbital region.—The interorbital cartilage (*EC.*) (Pl. 3, fig. 4) is long and narrow, it extends from the prootics to the anterior end of the skull, and its anterior part forms the rostrum. The interorbital part of this cartilage is rounded in cross-section, its ethmoid part is depressed dorso-ventrally. It has no lateral expansion in the anterior part of the orbit, such as is found in *Eurypharynx*, from which in the latter fish the *mm. obliqui* of the eye arise. In *Saccopharynx* there are two separate small cartilages (*EL.*) in this part of the orbit, and from these cartilages arise the *mm. obliqui*. It seems possible that these cartilages correspond to the lateral ethmoids; they are attached to the cranium by strong ligaments (*l.*) extending

anteriorly to the tip of the rostrum. There are no ossifications in the interorbital cartilage (no orbito-sphenoid).

The eye is situated more posteriorly than in *Eurypharynx* and the orbit is protected from above mainly by the anterior expansion of the sphenotic.

The floor of the orbital region (*m.*) between the interorbital cartilage and the sphenotics is membranous. Dorsally the brain extends over the orbital region.

The ethmoid or rostral region.—The ethmoid region of the cranium of *Saccopharynx* is elongated, forming a rostrum projecting in front of the orbits to more than a third the total length of the cranium. It is formed by the anterior part of the cartilage which divides the orbits ventrally. There is nothing in the uniform structure of this cartilage which would suggest that the ethmoid rostrum of *Saccopharynx* is movable and pendant, as Regan (1912 *a*, p. 348) described it.

Dorsally the rostrum is covered with a dermal bone (*ET.*) (Pl. 3, fig. 3). The position and the extension of the olfactory organs and nerves could not be examined owing to the poor condition of the specimen which I studied. There are no grooves in the cartilage for lodging these organs.

Along the ventral side of the rostro-interorbital cartilage, from its anterior end to about half the length of the orbital region, extends a very strong ligament which is inserted into the tips of the bones forming the upper jaw. This ligament is attached anteriorly and from the sides to this cartilage (the ligament had been removed when fig. 4 in Pl. 3 was made).

Cover bones of the neurocranium.—Beside the dermal parts of the pterotics and possibly of the sphenotics, a pair of frontals and a supra-ethmoid are found in the neurocranium of *Saccopharynx*.

The supra-ethmoid (*ET.*) (rostrale-postrostrale, Holmgren and Stensio) is a long and narrow bone extending from the tip of the rostrum and covering dorsally the whole of the ethmoido-rostral region. Its shape is shown in fig. 3, Pl. 3. Posteriorly it overlaps the anterior ends of the frontals.

The frontals (*F.*) (Pl. 3, fig. 3).—A large part of the cranium, in front of the epiotics up to the supra-ethmoid is covered dorsally by a single pair of large bones. They correspond, possibly, to both the parietals and frontals of *Eurypharynx*, and could thus be called fronto-parietals. But their development is unknown, and there is no proof for such a suggestion. The frontals meet each other at the medial line where they form a noticeable ridge. The dorsal ridges of the frontals, which are usually found in teleosts connected with the supra-orbital lateral line, are missing.

No nasals were found in the mutilated specimen which I studied; this does not prove, however, that the nasals are absent in *Saccopharynx*.

There is no vomer and no parasphenoid.—The ventral surface of the cranium of the specimen of *Saccopharynx* which I studied was undamaged along its medial line, and its examination shows clearly that the vomer and parasphenoid are absent in *Saccopharynx*.

(b) *The shoulder girdle and the skeleton of the pectoral fins* (text-fig. 14).

The lobes of the pectorals are large (in proportion to the size of the fin) and rounded, reminiscent of those of some Pediculati, though differing from them substantially in structure.

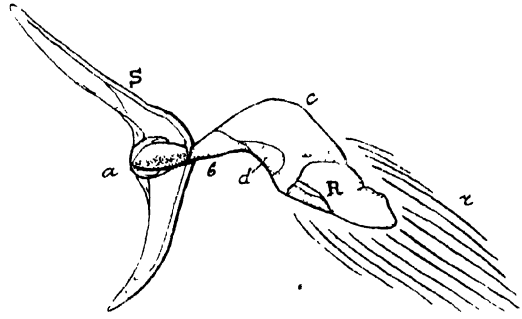
The skeleton of the shoulder girdle consists on either side of a single well-ossified V-shaped bone which is probably the scapular (*S.*), or scapular-coracoid. It is situated deep below the integuments and under the lateral muscles of the body. The scapulars on the left and right sides are completely disconnected from one another, and are not attached to the neurocranium by ligaments. The skeleton of the lobe is cartilaginous. On the lateral side of the scapular, where it bends, there is a well-formed groove for lodging the anterior cartilage of the lobe (*a*). This

cartilage articulates with the shoulder girdle laterally, not medially as in Pediculati (*cf.* Derjugin, 1910, pl. xxvii, fig. 15), and therefore the main bone of the shoulder girdle of *Saccopharynx* is not a cleithrum. In the specimen I studied it is not clear whether the cartilage (*b* in text-fig. 14), joining distally to the cartilage *a*, is a distinct element or has become separated from the latter by injury. The main part of the pectoral lobe projecting from the body consists of a rather large curved cartilage (*c.*), and of two distal cartilages, the radials (*R.*). The large curved cartilage (*c.*) has a subdivision (*d.*) which is not distinct. The radials (*R.*) do not articulate with the pectoral girdle and thus differ from all Actinopterygians.

The structure of the pectoral girdle and of the skeleton of the pectoral fin is so peculiar that it deserves careful study of better material than that in my possession.

The skeleton supporting the unpaired fins is generally similar to that of *Eurypharynx* and consists of similar elements (p. 327). I had no opportunity to study it in more detail.

The vertebrae.—As in *Eurypharynx* the vertebrae of *Saccopharynx* are ossified round their surface only ; the notochord is persistent through the vertebrae. Contrary to what is found in *Eurypharynx*, both the neural and haemal processes are present in all anterior vertebrae. The caudal part of the specimen which I studied was



TEXT-FIG. 14.—Skeleton of the pectoral girdle and pectoral fin of *Saccopharynx ampullaceus*. Left side, × about 6. Diagrammatic.

a., anterior cartilage supporting the lobe of the pectoral fin ; *b.*, part of the cartilage *a* separated from the latter by injury (or a separate element of the lobe ?) ; *c.*, the main cartilage of the lobe ; *d.*, indistinct subdivision in the cartilage *e* ; *R.*, two radials ; *r.*, fin rays (the fin rays in the specimen were broken and their number was not counted) ; *S*, the scapular or scapular-coracoid (well-ossified bone). Cartilages dotted.

not dissected, and thus the caudal vertebrae were not examined. Günther (1887, p. 259, pl. lxvi) described and figured two vertebrae of *Saccopharynx*.

The ribs, epineurals, epicentrals and pleurocentrals are absent.

4. *General Characteristics of Lyomeri.*

From the data found in literature and from the present very incomplete study, the Lyomeri can thus be characterized :—

As Prof. Hjort has discovered, the young Lyomeri are leptocephalus-like. Their body is deep, compressed from side to side and relatively short.

In specimens which have passed the leptocephalus stage, the body is much elongated, the tail being markedly longer than the trunk, tapering towards its posterior end. The anal and dorsal fins are long, extending to the posterior end

of the body. There are no ventral fins nor girdles. A mid-ventral fold extends in front of the anus to the membrane surrounding the branchial apparatus. The caudal fin is absent in large specimens, but 'very distinct' in small *Eurypharynx* (Zugmayer, 1911, p. 90). The pectorals are lobate. All the fin-rays are soft, flexible, not branched, not segmented; the left and right halves of the fin-rays are not fused together.

The cranium is small, articulating movably with the first vertebra. The jaws are very long. The rami of the upper jaw are attached at their symphysis to the ventral surface of the skull by a strong ligament. The anterior ends of the bones forming the upper jaw reach to the centre of the pupil and extend backwards to the vertical line of at least the 10th vertebra or further. The suspensorium is long and narrow, slanting slightly down and extending backwards almost parallel to the vertebral column. The branchial apparatus is separated from the cranium and from the lower jaw; the foremost visceral cleft being under the 12th vertebra, or further backwards. There are no bones or ligaments, nor differentiated muscles uniting the gill arches with the cranium or with the lower jaw. There is no slit separating the hyomandibular from the anterior part of the vertebral column, and the suspensorium is intimately united by integuments with the anterior vertebrae, so that the movements of both structures are co-ordinated. There are no ventral hyoid elements attached to the hyomandibular. The branchial chambers are imperfect and only partly covered from the outside by a fold of integument not supported by bones. Thus the external apertures of these chambers cannot be shut completely and the breathing process differs markedly from that usually found in Actinopterygians. The water is probably pumped into the gill pouches by special muscles which are situated medially to the branchial arches.

The ventral parts of the branchial arches, the ventral aorta and the heart are not movable anterio-posteriorly (as they usually are in fishes), and there are no elements of the skeleton for supporting and protecting the ventral aorta.

There is no branchiostegal fold. There are no gill-rakers.

The upper jaw is depressed by a muscle (*abductor mandibulae*), arising from the pterotic and inserting in the posterior end of the mandible.

The lateral line system has sensory organs set on papillae projecting from the surface of the body. There is no branch of the lateral line system along the lower jaw. The infraorbital branch of this system extends along the anterior part of the upper jaw. Behind this branch two more lines run parallel to the suspensorium, one from the hind edge of the eye to the mandibulo-quadrate articulation and the second from the hind edge of the eye to the base of the pectoral fin.

Two narrow stripes extend along the sides of the dorsal fin and are supposed to be luminous; no similar structures are known in other fishes. There are no scales.

The kidney is single. As in many other marine fishes, the glomerules Malpighi are absent (Nussbaum-Hilarowicz, 1923, in *Eurypharynx*). The gonoducts are well developed in small and not ripe specimens, uniting in an unpaired canal which opens on a small papilla between the vent and the urinal aperture; in ripe specimens the oviducts deteriorate and the eggs fall into the cavity of the body, and are shed through the pore which corresponds to the external orifice of the unpaired canal of young specimens (Nussbaum-Hilarowicz, 1923, p. 73). There are no pyloric appendages and no air bladder.

Cartilage bones and cover bones are present. The cartilage bones are only partly ossified on the surface. The bones are with cells (Nussbaum-Hilarowicz, 1923). The notochord persists through all vertebrae and throughout half the basioccipital. The vertebral centra are ossified with the neural and haemal processes. The distal ends of these processes are free and do not form arches. There are no ribs, epipleurals, epicentrals or pleurocentrals; no spines. Radials supporting the unpaired fins consist of two segments (according to Bertin three segments); from two to three radials correspond to one vertebra. One dorsal or anal fin-ray corresponds to

each radial. The pectoral girdle is separated from the cranium ; there is no cleithrum, supracleithrum, or post-temporal. The right and left parts of the pectoral girdle are completely separated from each other. There is only one ossification on each side of the pectoral girdle (scapular ?). The cartilage elements of the lobe of the pectoral fin join laterally to this bone (not medially). The radials do not articulate with the shoulder girdle, but with the basal elements of the pectoral lobe. The cranium is only partly ossified. Parts of the neurocranium are movably joined together. The lateral occipital articulate movably with the dorsal processes of the basioccipital, and the processes of the prootics with the ventral processes of the sphenotics. The brain case extends over the orbital region. There is no supraoccipital, and no ossifications corresponding to the lateral ethmoids ; there are no cartilage-opisthotics. No posterior not anterior myodomes ; no groove for lodging the olfactory organs. The interorbital cartilage is low with no ossifications. There is no orbitosphenoid, no basisphenoid, no alisphenoids. The intercalaries ('opisthotics' of some writers) are absent.

The structure of the visceral arches is unusual and their homologies are uncertain. As far as can be judged from the very incomplete study, this structure appears as follows.

The mandibular arch forms the upper and the lower jaws and the distal part of the suspensorium. There is no secondary upper jaw (maxilla, premaxilla). The dorsal part of the hyoid arch forms the proximal segment of the suspensorium, but the fate of its ventral part is not clear. This part is either entirely missing, or is situated in the septum behind the foremost visceral cleft. If the first suggestion is correct *Eurypharynx* has six branchial clefts ; if the second suggestion is proved to be correct, these fishes have a functioning ventral part of the pre-hyoid cleft and five branchial clefts in *Eurypharynx* and four in *Saccopharynx* *.

The upper jaw is well ossified and armed with teeth, it is apparently formed by the pterygo-palatine elements possibly fused anteriorly with the suborbitals. The infraorbital series of the lateral line system passes along the anterior part of this bone. The upper jaw bone lies medially to the *m. adductor mandibulae*, to the hyomandibular, the mandible and the quadrate ; its posterior end articulates with the medial side of the quadrate.

The rami of the upper jaw bone join together and are attached to the ventral side of the neurocranium at the vertical line of the centre of the eye.

The quadrate is intimately united with the hyomandibular. The mandible is well ossified medially and laterally, and bears teeth. Meckel's cartilage is small and restricted to the posterior part of the bone. The dermal ossifications of the lower jaw are not connected with the lateral line system. Their homologies are not clear.

The hyomandibular articulates with the ventral side of the cranium by a single condyle. The hyomandibular branch of the facial nerve passes out medially to the hyomandibular, and at about the same vertical level as the dorsal end of this bone. The *r. mandibularis internus* of this nerve perforates the hyomandibular. There is no *processus opercularis* ; no opercular fold or opercular bones are connected with the hyomandibular. There is no symplectic and no interhyal.

The branchial arches are not ossified, they are formed by semiarches not united ventrally by basal elements. The number of cartilages in these semiarches is not known ('three or four'.) There are no opercular bones : operculum, suboperculum, interoperculum and the branchiostegals are absent ; there is no preoperculum. The tendon of the *m. abductor mandibulae* is well ossified.

Two families : Saccopharyngidae and Eurypharyngidae.

SACCOPHARYNGIDAE : Four visceral arches bearing gills, five visceral clefts, the fifth almost closed. Vomer and parasphenoid are absent. Two small cartilages,

* See note on p. 287.

separated from the neurocranium, situated in front of the orbits, are present. The *mm. obliqui* arise from these cartilages. The ethmoido-rostral cartilage is long and narrow, covered dorsally by a supra-ethmoid. The anterior vertebrae with well developed haemal processes; the basioccipital with strong ventral processes. The foramen for the *n. vagus* passes between the basioccipital and the lateral occipital.

EURYPHARYNGIDAE: Five visceral arches bearing five holobranchs, six visceral clefts. Vomer and parasphenoid are present. There are no separate cartilages in front of the orbits, the ethmoido-rostral cartilage is broad and short. The *mm. obliqui* arise from the sides of this cartilage in the anterior part of the orbit. There is no supra-ethmoid. Only ridges on the ventral side of the anterior vertebrae present; similar low ridges on the ventral surface of the basioccipital present. The foramen for the *n. vagus* perforates the lateral occipital.

The Saccopharyngidae differ from Eurypharyngidae also by many other characters: structure of visceral clefts; number of vertebrae (no less than 138 in Saccopharyngidae, less than 115 in Eurypharyngidae); larger teeth in Saccopharyngidae. They differ also in proportions, position of the vent, shape of the caudal organ, etc.

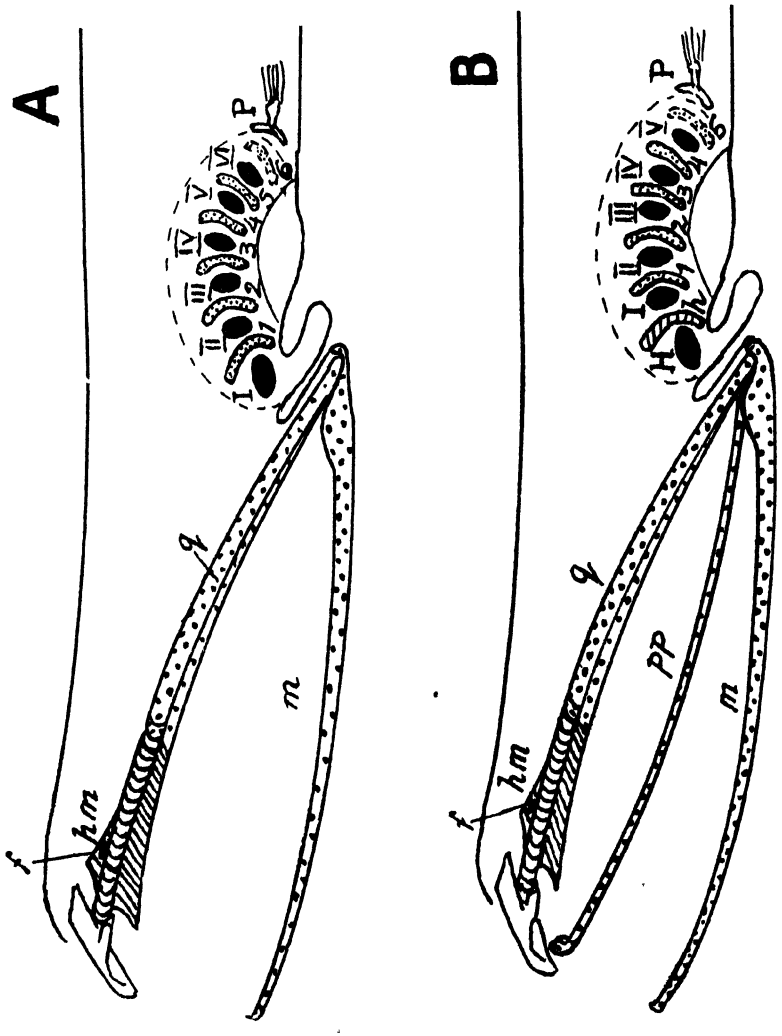
Each family is represented by one genus: *Saccopharynx* and *Eurypharynx*. A brief synopsis of the species of these genera is given in the first part of this paper.

5. *On the Monognathidae Bertin.*

From four adolescent specimens, Bertin (1936, 1938) described Monognathidae as a third family of Lyomeri. One of these specimens (the type of *Monognathus tåningi* Bertin, 'Dana' St. 1161, IV) has been earlier described and figured by Roule (1934, pp. 242, 243) as a semilarva of Lyomeri. According to Bertin the family Monognathidae consists of one genus *Monognathus*, with three species. Myers (1940, p. 141) subdivides the genus *Monognathus* into two genera, *Monognathus* and *Phasmatostoma*. However, as Berg (1940, p. 440) has already pointed out, there is no evidence that Monognathidae are related to Lyomeri. Specimens of this group are not obtainable and all that is known about them are Bertin's descriptions and figures. From these data Monognathidae differ from Lyomeri thus:

	LYOMERI	MONOGNATHIDAE
1. Visceral arches bearing gills	five or four	one (description) or none (figures)
2. Meckel's cartilage	present	absent (?)
3. Pterygo-palatine	present	absent
4. Lateral line system	present	absent (?)
5. Shoulder girdle	present	absent
6. Skeleton supporting the rays of unpaired fins	present	absent
7. Pectorals	present	absent
8. Supraoccipital	absent	present, very large (figures)
9. Separate lateral occipitals	present	absent
10. Basioccipital	present	absent (figures)
11. Prootics	present	absent (figures)
12. Orbitosphenoid	absent	present (description)
13. Alisphenoid	absent	present (description)
14. Light organs	present	absent

The descriptions and figures of Monognathidae do not always agree, and raise much doubt. For instance, in text-fig. 3 the *quadrate* (*sic*) is shown articulating with the middle line of the ventral surface of the neurocranium, where, according to



TEXT-FIG. 15.—Diagram of the visceral

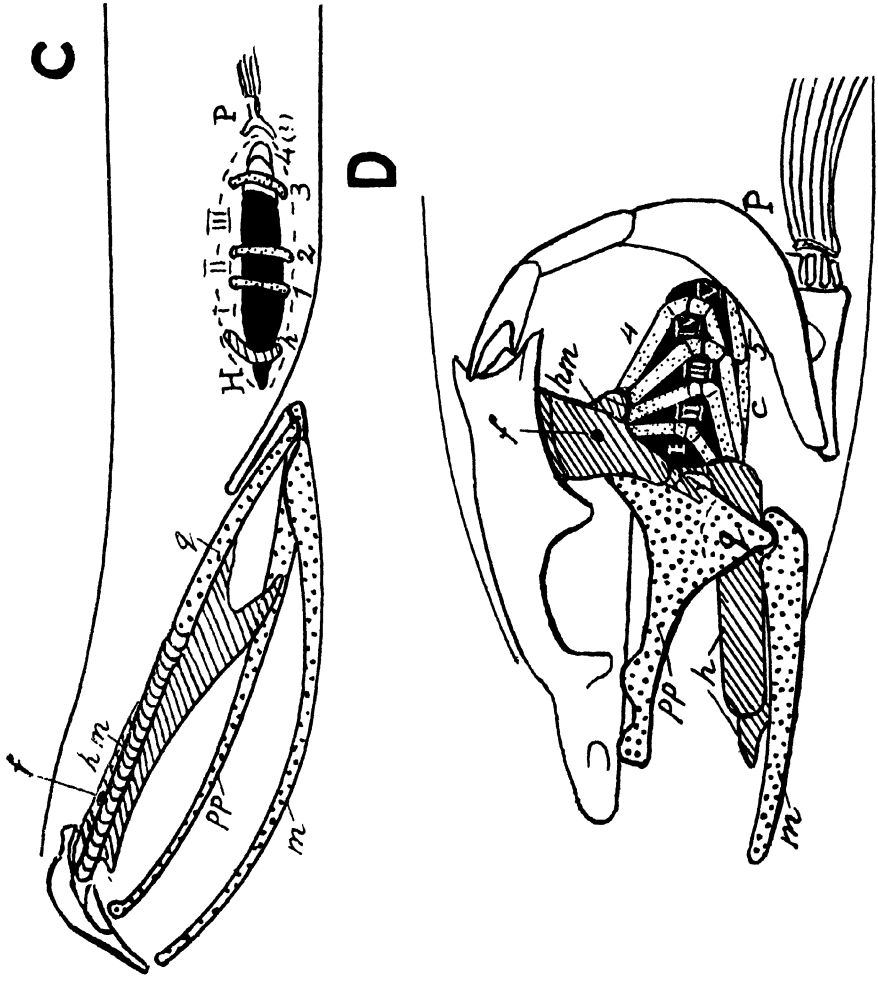
No dermal bones of the jaws and palate are shown. The bones of the suspensorium and of really are.

A. *Eurypharynx*, visceral skeleton as it is usually interpreted : no ventral elements of the hyoid the dermal maxillary and is therefore not shown in the diagram.

B. *Eurypharynx*, another interpretation of the visceral skeleton : the ventral elements of the the upper jaw, a prehyoid and five branchial clefts present.

C. *Saccopharynx*, interpretation of the visceral skeleton as in B, the two posterior branchial clefts

D. *Actinopterygian*.



arches of Lyomeri and Actinopterygians.

the jaws of Lyomeri are shown here shorter and heavier, and the gill apparatus larger than they

arch, no palato-pterygoid, six branchial clefts. The upper jaw is supposed to be formed by

hyoid arch support the septum behind the anterior cleft; the palato-pterygoid elements form

are reduced,

Bertin, a 'ptérotique' is found. Bertin (pp. 4, 5) describes the alisphenoids, an orbitosphenoid, and a single branchial arch in *Monognathus*, but in his figures all these elements are absent. Bertin does not show in his figures a number of most important elements of the skull, and completely ignores them in his description. These are :— the basioccipital, Meckel's cartilage, the vomer, the parasphenoid, the prootics, the basibranchials and the basihyal, the epi-, cerato-, hypo- and interhyals. This creates much uncertainty, and no judgement can be formed on Monognathidae. Even the 'main' character of Monognathidae, the absence of the upper jaw, does not seem certain. There is no evidence that the palato-pterygoid *cartilage* is absent in Monognathidae. Bertin (p. 5) stresses that he has not found any *bones* in the region of the upper jaw (palatines, pterygoids, premaxillaries, maxillaries), but he does not say that the cartilage corresponding to the auto-palatine or the metapterygoid is absent in Monognathidae. The method which Bertin used (clarifying with potassium and glycerine and staining with alizarin) shows the ossified parts only, but not the cartilages.

For the same reason his statement about a single branchial arch in Monognathidae does not seem convincing.

The species of the genus *Monognathus* differ from one another more than species usually do. Thus, *M. bruuni* (text-fig. 2) has a hyostylic skull, while the skull of *M. tåningi* (text-fig. 3) is autostylic!

III. The Position of Lyomeri in the System of Fishes.

1. *Opinions of earlier writers.*

As I have already stressed in this paper, the structure of Lyomeri is imperfectly known ; the homologies of the most important parts of the skeleton are still obscure ; little is known about the relation of the visceral arches to the cephalic nerves ; the development of these fishes has never been studied ; and it is not known whether the 'leptocephalus'-like larva of Lyomeri corresponds to that of Anguillidae or whether their likeness is only a superficial one. Thus speculations about the systematic position, origin and relationship of Lyomeri are more guesses than opinions or theories.

With the exception of Nussbaum-Hilarowicz (1923), all writers hold that Lyomeri belong to the group of fishes which used to be called 'Teleostei', and that the peculiar structure of Lyomeri must be considered as the result of atrophies, deformation, adaptations, hypertrophies, degenerations, specialization and degradation provoked by the struggle for existence, disharmony between different organs, unusual surroundings and habits, lack of competition, ultra-violet rays, vitamins*, and other commodities which the teleostean fishes usually enjoy but of which 'the rachitic offshoots of evolution' are deprived. From this point of view the Lyomeri are abnormalities or 'normalized abnormalities', and their peculiarities have but little significance, being acquired secondarily, obscuring the true relationship and position of Lyomeri among the Neopterygians.

This opinion on the nature of Lyomeri appears to be almost unanimous. But there is a great variety of ideas among ichthyologists about the place which the Lyomeri occupy in the system of Neopterygii and about the grade attributed to the group of Lyomeri. This group has had all the taxonomic ranks from a species to an order, and was associated with many different orders of Neopterygii.

* It might be mentioned that the contents of the antirachitic vitamin in the fats of *Sebastes marimus* (which prospers in the Barentz Sea at the latitudes of 69°–70° N. at a depth of 200 m.) is sufficient for commercial exploitation of these fats for medical purposes (compare Parr, 1937, pp. 27, 28).

Most writers look upon Lyomeri as relatives of Apodes (Cuvier, 1829, p. 355). Günther (1880, p. 670) ranks them as a genus of the family Muraenidae (next to *Cyema*); Boulenger (1904*a*, p. 168; 1904*b*, p. 603) and Brauer (1906, p. 134) as a family of Apodes; Jordan (1923, p. 134) as a suborder of Apodes; Gill and Ryder (1883) as an order close to Apodes. The two latter opinions were shared by many writers. But there were also different opinions. Regan (1912*a*, p. 348) found that 'the whole structure of Lyomeri is quite unlike that of Apodes', and placed the Lyomeri (an order) next to Iniomi, emphasizing specially the likeness of Lyomeri with the Synodidae (?=Synodontidae); later Regan (1925, p. 57) suggested that the Giganturidea are the nearest relations of Lyomeri. Berg (1940, p. 439) adopted this view. Gregory (1933, p. 213) expressed the belief that the skeleton of *Cetomimus* (order Iniomi) has more resemblance to that of Lyomeri, and put the Lyomeri back next to Iniomi. Goodrich (1930, p. xviii) placed the Lyomeri between Iniomi and Apodes. Zugmayer (1913, p. 4) found that the skull of *Symbranchia* (order Symbranchii) as figured by Regan (1912*b*), reminded him of the skull of *Eurypharynx* and suggested that the Lyomeri are a degenerate group related to the Symbranchii. Mitchill (1824, p. 86) thought that *Saccopharynx* and *Stylophorus* (order Allotriognathi) are identical. Vaillant (1882, pp. 1226–1228) found that *Eurypharynx* resembles many fishes: Stomiatidae (order Isospondyli), Scopelidae (order Iniomi), Macruridae (order Anacanthini) and some other fishes belonging to different orders of Teleostomes. Vaillant (1888, p. 14) placed the Lyomeri between the Macruridae (order Anacanthini) and the Pleuronectidae (order Heterostomata). Bertin (1934, pp. 6, 7) believed that the Lyomeri are related to the Lophobranchii (order Ostariophysi)* but considers them as a sub-order of the order Apodes. Thus, a great many Neopterygians with an elongated body and a large mouth were considered as probable relatives of Lyomeri.

Nussbaum-Hilarowicz (1923, p. 74) took another point of view and on the grounds that the Lyomeri have no opercular bones proposed to consider them as a group opposed to all other fish-like animals with an operculum.

2. *Comparison of Lyomeri with Osteichthyes.*

The Lyomeri agree with the Osteichthyes only in a few features; they have replacement and dermal bones, and the hyomandibular branch of the facial nerve passes out medially to the hyomandibular. The skull is hyostylic, and the *r. mandibularis internus* of the facial nerve reaches the mandible.

Contrary to Osteichthyes in Lyomeri: the bone acting as the upper jaw is situated medially to the *m. adductor mandibulae* and to the quadrate, and is probably a pterygopalatine element. The secondary upper jaw (premaxillary and maxillary) is absent. The bones of the lower jaw are not connected with the mandibular branch of the lateral line system, and this branch is apparently missing in Lyomeri. The junction between the hyomandibular and the quadrate differs from Osteichthyes, being much more intimate; the rounded flange of the hyomandibular joins by harmony to the exactly similar flange of the quadrate, and the ossified lamellae of both elements are fused together. There is no symplectic. There is no opercular process of the hyomandibular. There are no opercular elements (preoperculum, operculum, suboperculum, interoperculum, branchiostegals absent).

* Bertin (1934, p. 7) attaches great importance to the fact that no glomerules Malpighi are found in *Eurypharynx* (as was shown by Nussbaum-Hilarowicz 1923), and that these glomerules are also absent in the Lophobranchs (as was shown by Huot, 1897, 1902; Verne, 1922). However, as glomerules Malpighi are absent, or much reduced in number, in many marine fishes, belonging to no less than twelve different families and to five different orders (Edwards, 1928, 1929; Edwards and Condorelly, 1928; Marshall and Grafflin, 1928; Marshall and Smith, 1930; Nash, 1931; Oordt, 1938), it does not seem clear why Bertin compares the Lyomeri with the Lophobranchs only.

The right and left elements of the branchial arches are separated from each other (there are no ventral basal elements uniting them), *i. e.* they are not united as in Osteichthyes. The branchial integumental folds cover only partly the visceral clefts and the gills ; the branchial chambers are not properly formed and cannot be shut. The current of water to the gills is apparently regulated by muscular sphincters lying medially to the branchial arches. The branchial arches are not connected with the cranium, nor with the vertebral column. The septa between the branchial clefts are not reduced to <-shaped branchial arches. There are no olfactory grooves in the neurocranium.

The cover bones of the dorsal side of the cranium are unusual and their homologies with those of Osteichthyes are uncertain. The vomer and the parasphenoid are either absent or much reduced in size, and the parasphenoid, if present, has no lateral (ascending) processes.

The pectoral girdle is not united with the cranium, its left and right sides are not united ventrally and there is no cleithrum. The radials of the pectoral fins do not articulate with the shoulder girdle, but their basal elements differ from the Crossopterygian type.

The Lyomeri have no ribs, the neural processes of the vertebrae do not meet and thus do not form arches ; they bear no unpaired spines. The dermal processes of the fin-rays are unsegmented ; there is no sign of lepidotrichia. The ventral fold of the anal fin extends in front of the anus up to the branchial fold (it is not supported by rays in front of the vent).

The *m. genio-hyoideus* (=*m. protractor hyoidei*), the presence of which Holmquist (1910, p. 23) considers a character of the class of bony fishes, is absent in Lyomeri.

The Lyomeri have no scales and no air-bladder.

Contrary to all Osteichthyes the Lyomeri have *six visceral clefts and five holobranchs* (in *Saccopharynx* the posterior cleft is rudimentary). This fact can be interpreted in two ways : (1) that the Lyomeri have *six branchial clefts* with five holobranchs, and have *no ventral elements of the hyoid arch*, (2) that these fishes have a functional ventral part of the prehyoid cleft, that the first holobranch belongs to the septum between the prehyoid and the first branchial clefts, and that the ventral elements of the hyoid arch are situated behind the foremost visceral cleft *. If the second suggestion is correct the Lyomeri recall more the Acanthodian fishes, as the latter were described by Watson (1937), than Osteichthyes. But since Holmgren's revision of Acanthodians (Holmgren, 1942), no such comparison seems possible. Thus, a comparison of Lyomeri with Osteichthyes shows that they differ fundamentally from Osteichthyes, and could hardly be referred to this class without altering substantially the characteristics of the class Osteichthyes.

The characters of Lyomeri which differentiate them from Osteichthyes cannot be rejected as unimportant, or treated as merely a degeneration secondarily acquired. The Lyomeri are large (up to six feet long) fishes, freely swimming in the ocean, they are widely distributed through the sea, and are not at all uncommon (Hjort, 1912, p. 96). They live among most strongly armed and most voracious fishes, and the *Saccopharynx* feeds upon large fishes. None of the Osteichthyes found together with the Lyomeri (or even in the stomachs of Lyomeri) had lost the characters of their class, or acquired new and fundamentally different ones.

However, as among Osteichthyes there are some fishes with characters diverging from those of their class, it would be perhaps of interest to compare some of them with Lyomeri.

* See note on p. 287.

3. *Comparison of Lyomeri with some Osteichthyes diverging from the type of the class.*

There are forms among the Osteichthyes which have some features which do not agree with the diagnosis of their class and have some likeness with Lyomeri. But there is no Osteichthyes with six visceral clefts and five holobranchs, and there are no Osteichthyes in which the features disagreeing with the diagnosis of this class would predominate over those which do agree with the diagnosis.

Presence of a ventral prehyoid cleft.—A prehyoid cleft (between the mandible and the ventral elements of the hyoid arch) is not closed in all fishes of the family Malocosteidae (Order Isospondyli); this cleft is most likely of secondary origin (Tchernavin, 1946). In other respects the Malacosteidae fit into their class.

Palato-pterygoid elements acting as the upper jaw, while the secondary upper jaw is absent.—This was described (Trewavas, 1933, p. 608) in *Opisthoproctus soleatus* (order Isospondyli) *. In other respects *Opisthoproctus* agrees with the Actinopterygian type. The closely allied *O. grimaldii* (Gregory, 1933, p. 150) has a small maxillary bone.

Less clear is the case of *Muraena*. The upper jaw of this fish is not enclosed in a fold of integuments and its relations to the neurocranium and the mandibular arch are not clear. Owen, 1846, p. 30; 1866, p. 118; Bleeker, 1853, p. 299; 1864, p. 9; Boulenger, 1904 *b*, p. 600; Kyle and Ehrenbaum, 1926, p. 58, consider it as an element of the palato-quadrate; other writers hold that the upper jaw of Muraenidae is formed by the maxillary †. However, the criticisms of Owen's view (Regan, 1912 *c*, footnote on p. 378; Gregory, 1933, p. 203) are not based on a proper morphological investigation, nor on a study of the development of Muraenidae, and are not convincing. It seems that a revision of the structure of Muraenidae is desirable and it would be premature to discuss their structure here.

A hyomandibular having no opercular process is found in Chondrostei and in a few other Actinopterygii: in *Gigantura*, order Giganturoidea (Regan, 1925, fig. 2), and *Cyema atrum*, order Apodes (Trewavas, 1933, pl. i, fig. B).

Very little is known about the structure of the *ventral hyoid elements* and about their relation to the hyomandibular in the latter two fishes. According to Trewavas (1933, p. 603, fig. 2) there is a 'ventral nodule on each side of the ventral part of the hyoid of *Cyema*'; this nodule is situated ventrally and anteriorly to the quadrate. But the method of study used by Dr. Trewavas did not show the unossified part of the hyoid arch. According to Regan (1925, p. 56), in *Gigantura* the ventral hyoid elements 'appear to be unossified'; no more details are given.

Cyema is apparently the only Osteichthyes in which the opercular bones are possibly entirely missing. There is no preoperculum and no suboperculum (Trewavas, 1933, p. 603); the 'interoperculum' described by Trewavas is the ossified tendon of the *m. abductor mandibulae*, and thus can hardly be homologized with the interoperculum; it may correspond to a similar bone in Lyomeri (p. 331). The operculum is possibly also absent in *Cyema*. According to Trewavas: 'Its [of the hyomandibular] posterior edge bears an approximately triangular lamina, continuous with it but delimited by a structural line. At its upper end this lamina has the relations of an operculum and it may represent this bone, which is not present as a distinct element'. This lamina is not enclosed in a fold of integuments; the large

* Parr (1937, pp. 30, 31) has found in the anterior part of the snout of *O. soleatus* a thin, somewhat sculptured scale. He thinks that it represents the maxillary. This remains to be proved.

† Kesteven (1926, pp. 133, 135) apparently supports Owen's point of view on the nature of the upper jaw of *Muraena*. But the names of bones used by Kesteven seem somewhat obscure to me, and I could not follow his method of proving the homologies of these bones in fishes.

m. abductor mandibulae arises from its medial side ; it lies medially to the *m. adductor mandibulae*, which covers it completely. These features suggest that this lamella is more like a part of the hyomandibular than an operculum.

It is worth mentioning that *Cyema* has several more characters in common with Lyomeri. The supraoccipital is absent, the lateral line has filaments projecting from the body, the branchial fold surrounding the branchial clefts is disconnected with the hyomandibular. The hyomandibular articulates with the neurocranium by a single condyle. The mandible of *Cyema* is (as in Lyomeri) lowered by a special muscle, *m. abductor mandibulae*. (However, it seems uncertain that these muscles are homologous in these two groups. In Lyomeri the *m. abductor mandibulae* arises from the lateral side of the pterotic and lies laterally to the hyomandibular ; in *Cyema* it arises from the medial side of the hyomandibular and lies medially to the suspensorium.) The parasphenoid of *Cyema* has no ascending processes. But in spite of many common characters, the main features of *Cyema* differ from those of Lyomeri. The upper jaw of *Cyema* is formed by the maxilla and premaxilla and lies laterally to the *m. adductor mandibulae*, to the quadrate and to the mandible. *Cyema* has five branchials clefts and four branchial arches bearing four holobranchs. The main bone of the shoulder girdle is a cleithrum, the rami of which join ventrally ; the radii of the pectoral fins are not divided from the pectoral arch by basal elements. Thus the resemblance of *Cyema* to Lyomeri is apparently not due to a common origin.

Berg (1940, p. 439) mentions that *Gigantura* has no opercular bones, but this statement is certainly due to some misunderstanding. *Gigantura* has a well-developed opercular fold at the posterior edge of the hyomandibular ; this fold is indubitably supported by dermal bones. *Gigantura* has also a preoperculum (Regan, 1925, p. 56).

Unsegmented fin-rays (ceratotrichia) are found in embryonic fins of all Teleostoeans (Goodrich 1904, p. 473 ; 1930, p. 98) and such rays have also been described in the dorsal and anal fins of adult bony fishes.

A ventral mesial fold (not supported by rays) in front of the vent has been found in young Trichomycterinae (Tchernavin, 1944, p. 246).

The likeness of Lyomeri supposed by some writers with other Actinopterygii is not discussed here, for it seems obvious that the suggested similarities of their features are not real, but due to the insufficient study of Lyomeri.

IV. Summary.

Although some of the details of the structure of Lyomeri have been rather carefully studied, as for instance the minute structure of the gut, kidneys, of some bones and cartilages by Nussbaum-Hilarowicz, and the proportions of parts of the body by Bertin, the main characters of Lyomeri have not attracted the attention of scientists and the systematic position of the group is most uncertain.

The Lyomeri have a branchial apparatus built differently from other fishes ; the Lyomeri have no proper gill cover and no bones supporting such cover. In *Eurypharynx* there are *six* functional visceral clefts and *five* holobranchs (in *Saccopharynx* the hind cleft and the hind gill are reduced). The bone forming the upper jaw of Lyomeri lies medially to the hyomandibular, mandibular and the quadrate. The radials of the lobate pectorals articulate with the basal cartilages of the lobes but not with the pectoral girdle. The rays of the fins of Lyomeri are ossified, but soft and not segmented. The disposition of the series of the lateral line on the head is unusual. There is a series along the edge of the upper jaw, a series along the suspensorium, and one parallel to the suspensorium along the cheek, from the orbit to the posterior end of the opercular fold. There is no lateral line along the mandible.

Several more characters of Lyomeri stress the peculiarity of this group. The Lyomeri have no supraoccipital, and no lateral ethmoids ; the prootics of *Eurypharynx* extend anteriorly into the interorbital septum beyond the hypophysis and the trigeminus-facialis ganglion ; parts of the neurocranium are movably articulated ;

the cover bones of the roof of the cranium are unusual; there are no vomer and parasphenoid in *Saccopharynx* (these bones are present, but much reduced in *Eurypharynx*).

It seems possible, from the present study, that the upper jaw of Lyomeri is formed by the elements of the mandibular arch, that the anterior visceral cleft of Lyomeri is not a branchial but a prehyoid cleft, and that the cartilages supporting the septum behind this cleft are the 'missing' ventral elements of the hyoid arch*.

However, as in the specimens studied by me the cephalic nerves are partly lost their course could not be followed.

Thus these two main features of Lyomeri still remain uncertain.

An attempt at a general characterization of Lyomeri and of the two families of this group is made in Part II of this paper. In Part III a brief comparison of Lyomeri with the Osteichthyes generally, and with some peculiar Actinopterygians, is given.

In Part I the specimens of Lyomeri of the British Museum are described in some detail, their systematic position is discussed, and a brief revision of the species of *Saccopharynx* and *Eurypharynx* is given.

This work was done in rather an uncomfortable time and conditions. It was much delayed by the absence of books, and of many fishes preserved in the British Museum which had been evacuated for safety, and by the lack of various other facilities.

All the drawings and diagrams were made by the writer.

The system of fishes used here for the main groups is that adopted by Forster-Cooper (1940), and for the orders that used by Regan (1929).

The names of parts of the skeleton used here are mainly as used by de Beer (1937); references to the terminology of Holmgren and Stensio (1936) are also given.

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* See note on p. 287.

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EXPLANATION OF THE PLATES.

PLATE 2.

Fig. 1. Right branchial chamber of *Eurypharynx*. Side view. ×10. Diagrammatic.

The branchial fold of integuments is cut off. *B.*, branchial chamber; *J.*, posterior end of the quadrate and of both jaws; *P.*, pectoral fin; *Ph.*, pharyngeal fold; *V.*, anterior part of the belly.

Fig. 2. Left branchial chamber of *Saccopharynx ampullaceus*.

The branchial fold of integuments cut off. The branchial filaments in the specimens from which the figure is made were partly broken, and their number was not counted. Apparently each arch bears one hemibranch only.

Semi-diagrammatic. ×3·5.

PLATE 3.

Figs. 1 & 2. Neurocranium of *Eurypharynx pelicanoides* (fig. 1, dorsal view; fig. 2. ventral view.) Diagrammatic. ×7.

Text-fig. 11 the parasphenoid is removed from its place and shown at the side of the cranium at exactly its level.

B., basioccipital; *C.*, ethmoido-interorbital cartilage; *E.*, epiotic; *F.*, frontal; *FO.*, foramen for the vagus and glossopharyngeus nerves; *H.*, hyomandibular; *L.*, lateral occipital; *N.*, nasal; *O.*, eye; *P.*, prootic; *PA.*, parietal (?); *PT.*, pterotic; *PS.*, parasphenoid; *S.*, sphenotic; *V.*, vomer; *VT.*, first vertebra.

Cartilages dotted, bones shadowed with irregular lines, those with much cartilage seen through the perichondral ossifications, shadowed by lines with dots; eye muscles marked by transverse lines; nerves white. For cranial nerves of *Eurypharynx* see text-fig. 8.

Figs. 3 & 4. Neurocranium of *Saccopharynx ampullaceus* (fig. 3, dorsal view; fig. 4, ventral view). Diagrammatic. ×5.

B., basioccipital; *BD.*, dorsal process of the basioccipital; *BV.*, ventral process of the basioccipital; *c.*, cartilage between the cartilage-pterotic, sphenotic and prootic; *E.*, epiotic; *EC.*, ethmoido-interorbital cartilage; *EL.*, separate cartilage at the anterior corner of the orbit from which the *mm. obliqui* arise; *ET.*, supra-ethmoid; *F.*, frontal (?); *L.*, lateral occipital; *P.*, prootic; *PT.*, pterotic (cartilaginous and dermal); *S.*, sphenotic; *f.*, foramen for the nerves of the vagus group; *l.*, ligament uniting the cartilage *EL.* with the rostrum; *n.*, *n. trigeminus*; *m.*, membrane between the interorbital cartilage, sphenotic and prootic. Cartilage dotted; bones shadowed with irregular lines, those with much cartilage seen through the thin superficial ossification shadowed with lines and dots; ligament *l.* shadowed with transverse lines.

Fig. 1.

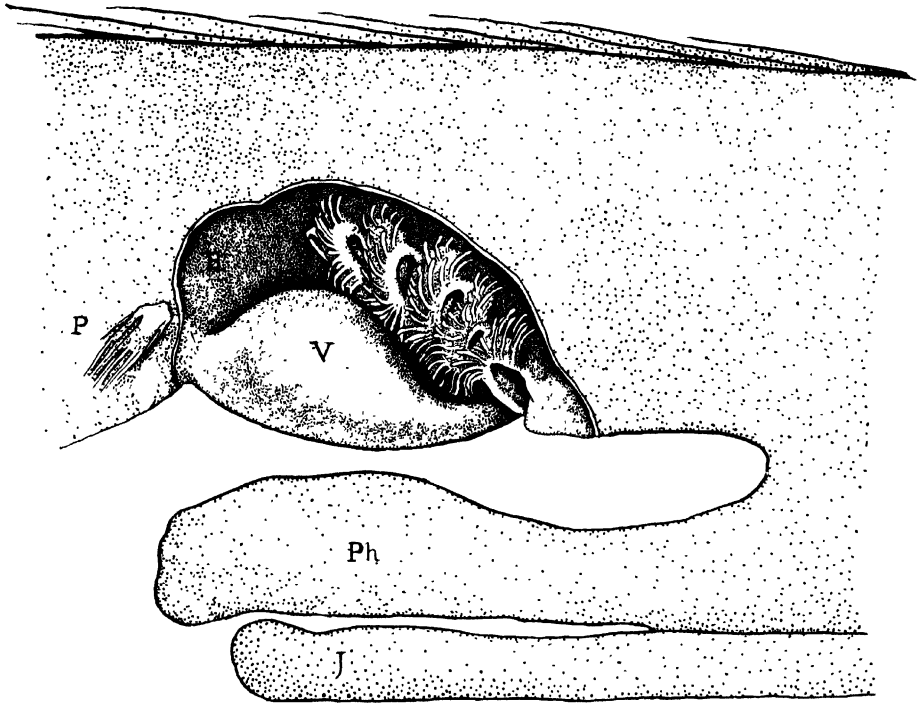
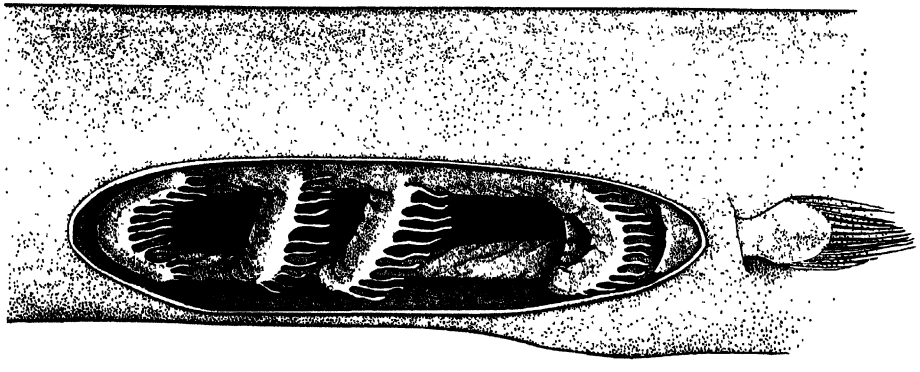


Fig. 2.



BRANCHIAL CHAMBER IN EURYPHARYNX AND SACCOPHARYNX.

Fig 1.

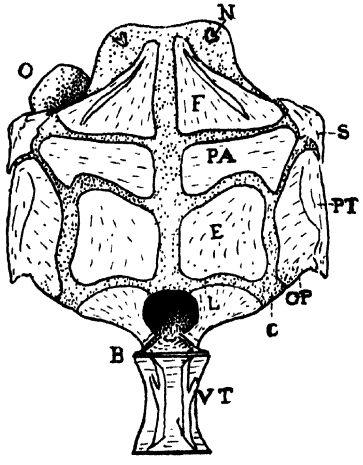


Fig 2

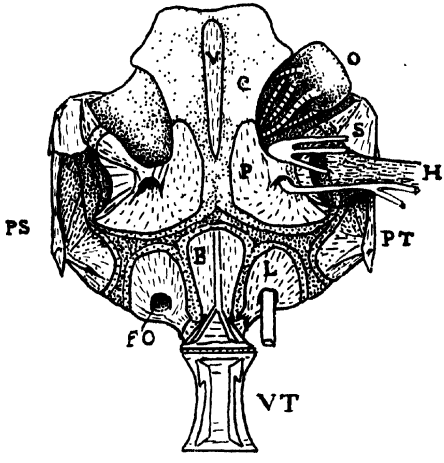


Fig. 3

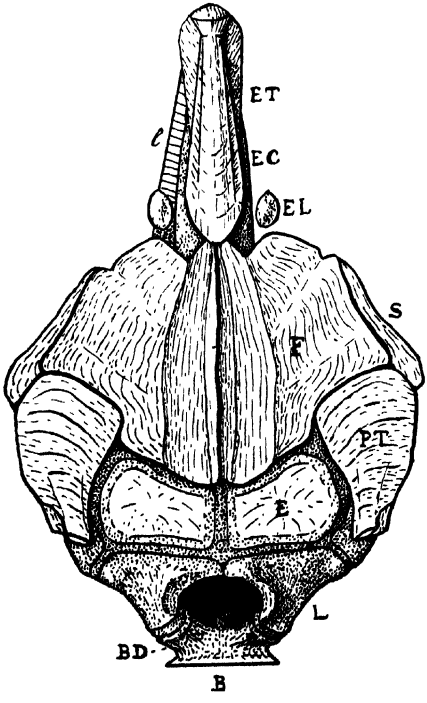
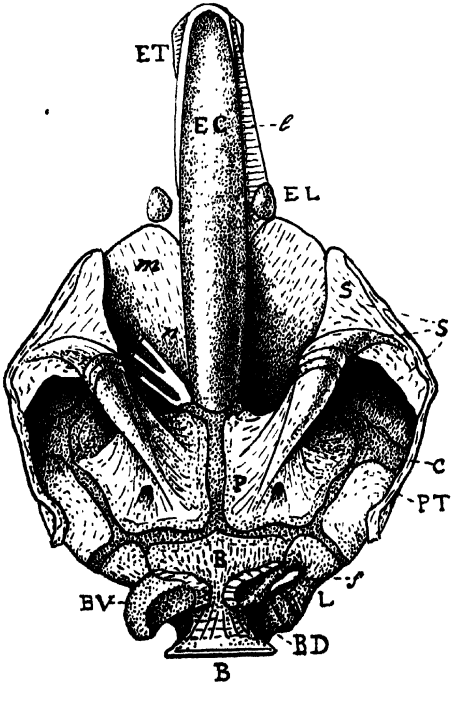


Fig 4



NEUROCRANIUM OF EURYPHARYNX AND SACCOPHARYNX.

The Head Glands of Snakes, with remarks on the Evolution of the Parotid Gland and Teeth of the Opisthoglypha.

By MALCOLM SMITH and A. D'A. BELLAIRS.

(PLATES 4 & 5, and 27 figures in the text.)

[Read 22 June 1944.]

INTRODUCTION.

The literature on this subject is extensive, but scattered. Reasonably accurate accounts of the topography of the head glands were made by early workers such as Duvernoy (1804), Cloquet (1821) and Schlegel (1837). Substantial contributions have subsequently been made by West (1895, 1898), Neimann (1892), Martin (1899), Haas (1930), Radovanovic (1935) and Schwarz-Karsten (1937), while a general survey of the subject has been made in the important monograph by Phisalix, 'Des Animaux venimeux et venins' (1922). The subject has also been reviewed by Fahrenholz in Vol. 3 of the 'Handbuch der Vergleichenden anatomie der Wirbeltiere', edited by Bolk and others (1935), and by Smith in his account of the reptiles of British India (1943). Nevertheless, there is a remarkable scarcity of accurate accounts of the site and manner of termination of the gland ducts based on microscopic examination of serial sections, and even the topographical accounts of the glands themselves are often somewhat ambiguous. An attempt has been made to remedy this in the present survey, in which data, based on microscopical examination of sections, have been incorporated. No investigation of the fine histological structure of the glands has however been made in this article, which deals only with the gross morphological characteristics of these structures.

MATERIAL AND METHODS.

The bulk of the material consisted of whole specimens preserved in spirit which were collected by one of us in Siam. Other spirit material from the collection in the British Museum was made available through the courtesy of Mr. H. W. Parker of that Institution. These specimens were examined by dissection under the binocular microscope. Serial sections through heads of a number of species were also available through the kindness of Prof. J. D. Boyd of the Anatomy Dept. of the London Hospital Medical College. We are also indebted to Mr. F. R. Parrington of the Zoology Museum in Cambridge, Dr. R. W. Haines of the Anatomy Department at St. Thomas's Hospital, Mr. K. C. Richardson of University College, and Dr. L. E. Glynn of University College Hospital, for the loan of specimens and help in their preparation.

A complete list and particulars of all the material examined is given at the end of this account.

NOMENCLATURE.

There has been some confusion in the nomenclature of these glands, especially with regard to the parotid or venom gland of the Opisthoglypha, the anterior temporal gland, and the Harderian gland of the eye. Glandular tissue is very abundant in the ophidian head, a development doubtless associated with the feeding habits of these reptiles, which involve abundant salivation,

EXPLANATION OF LETTERING.

add.m.ext.ant.	muscle adductor mandibulae temporalis externus anterior.
add.m.ext.med.	muscle adductor mandibulae temporalis externus medialis.
add.m.ext.post.	muscle adductor mandibulae temporalis externus posterior.
a.t.g.	anterior temporal gland.
a.t.s.	anterior wall of tongue sheath.
b.	brille.
cbl.	cerebellum.
cbr.	cerebral hemispheres.
ch.	choroid.
c.J.O.	cartilage of Jacobson's Organ.
corn.	cornea.
d.	dentine.
d.a.t.	duct of anterior temporal gland.
d.Hd.g.	duct of Harderian gland.
d.i.l.g.	duct of inferior labial gland.
d.J.O.	duct of Jacobson's Organ.
d.md.g.	duct of mandibular gland.
d.n.g.	duct of nasal gland.
d.sl.g.	duct of sublingual gland.
d.spl.g.	duct of superior labial gland.
d.spl.g'.	duct of enlarged posterior part of superior labial gland.
d.v.g.	duct of venom gland.
d.v.g'.	duct of venom gland (lower part).
dy.	dentary.
e.	enamel.
e.f.m.	epithelium of floor of mouth.
f.	poison fang.
fr.	frontal bone.
Hd.g.	Harderian gland.
i.l.g.	inferior labial gland.
J.O.	Jacobson's Organ.
l.	lens.
l.can.	lachrymal canaliculus.
l.d.	lachrymal duct.
l.j.	lower jaw.
lig.zyg.	ligamentum zygomaticum.
M.	Meckel's cartilage.
md.g.	mandibular gland.
m.l.j.	musculature of lower jaw.
m.o.	medulla oblongata.
mu.	musculature.
mx.	maxilla.
n.	nostril.
na.	nasal bone.
n.c.	nasal cartilage.
n.con.	nasal concha.
n.cv.	nasal cavity.
n.g.	nasal gland.
n.g'.	nasal gland (part within concha).
n.p.	nasal pad.
o.b.	olfactory bulb.
od.	odontoblasts.
o.e.	olfactory epithelium.
ol.l.	olfactory lobes.
o.n.	olfactory nerves.
op.l.	optic lobes.
p.	pulp of tooth.
pa.	parotid gland.
p.b.	pineal body.
p.l.s.	posterior labial scale
p.m.g.	pre-maxillary gland.
r.f.	reserve fang.
b.s.s.	sub-brillar space.
sc.	sclerotic.
sl.g.	sublingual gland.
smx.	septomaxilla.
sp.l.g.	superior labial gland.
spr.l.g.	supralingual gland.
t.	teeth.
t.c.	tissue condensation around fang.
t.m.	teeth of maxilla.
to.	tongue.
t.p.m.	teeth of posterior maxilla (enlarged).
tr.	trabecula.
trach.	trachea.
u.j.	upper jaw.
v.	vomer.
v.g.	venom gland.

We recognize the following glands :—

(1) Superior labial.
(2) Pre-maxillary or rostral.
(3) Parotid, restricted here to the modified posterior part of the superior labial gland in the Aglypha and the Opisthoglypha.
(4) Venom gland of Viperidae and Elapidae.
(5) Anterior temporal.
(6) Harderian.
(7) Inferior labial.
(8) Nasal.
(9) Mandibular.
(10) Sublingual.
(11) Supralingual.

FIG. 1.

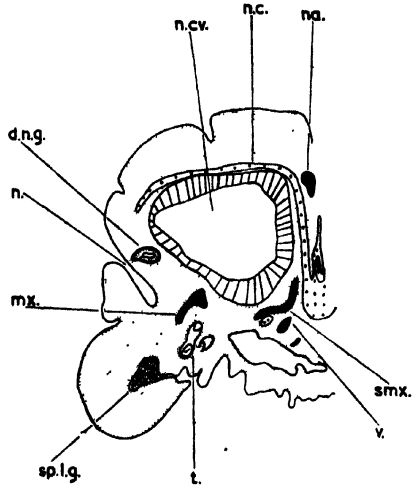


FIG. 2.

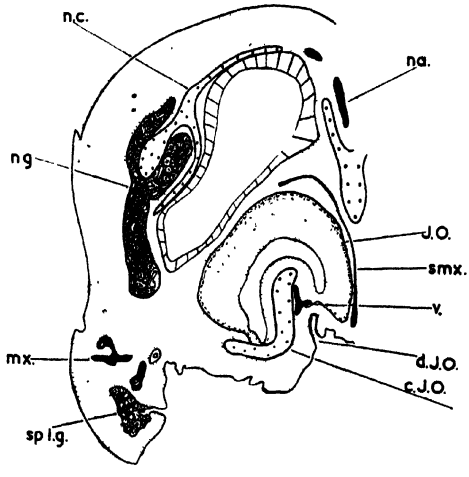


FIG. 3.

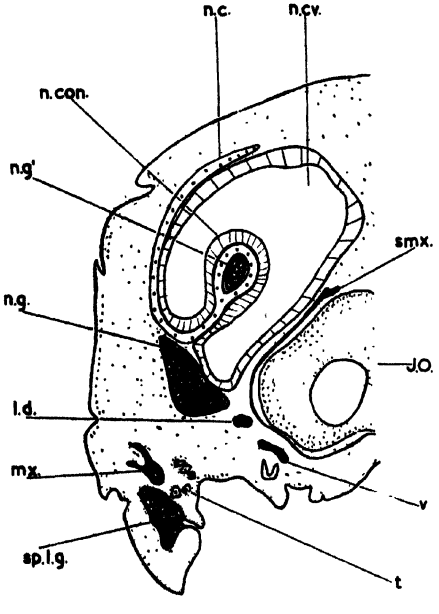


FIG. 4.

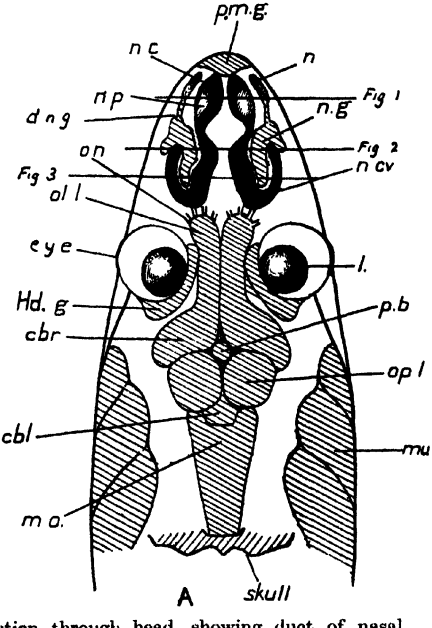


FIG. 1.—*Thamnophis sirtalis.* Transverse section through head, showing duct of nasal gland opening into the posterior aspect of the nostril, and duct of superior labial gland.

FIG. 2.—*Thamnophis sirtalis.* As fig. 1, but further back, showing nasal gland becoming incorporated into nasal concha.

FIG. 3.—*Thamnophis sirtalis.* As fig. 2, but a few sections further back, showing nasal gland completely incorporated into nasal concha.

FIG. 4.—Diagram of horizontal section through head of a Colubrine Snake to show nasal cavity and approximate planes of section in figs. 1–3.

These terms may also be applied to the corresponding structures in lizards, where however other glands not present in snakes also occur. The small integumentary glands present in certain burrowing snakes (e.g. *Typhlops*) are not considered in this review. Reference to Plates **4** and **5** illustrates the topography of these glands in various species of snakes.

(1) *The Superior Labial glands.*

These glands have been identified in all the species from which microscopic sections have been examined, though in some types such as the Boidae and *Xenopeltis* they are so weakly developed as to be almost invisible under the dissecting microscope, and are represented only by a chain of scattered acini lying in the labial connective tissue. In most snakes they are well developed, however, and consist of strips of glandular tissue divided transversely into lobules by fibrous trabeculae, bordering the mouth on either side and lying immediately beneath the labial scales. Each lobule discharges by a separate duct opening inside the labial margin lateral to the bases of the teeth (figs. 1–4). This represents the primitive unmodified condition of these glands, and is found in most Boidae, in *Pareas* (= *Amblycephalus*) *carinatus*, in certain Aglyphs such as *Oligodon cyclurus*, *Macropisthodon rhodomelas* and *Elaphe radiata*.

(2) *The Pre-maxillary or Rostral gland.*

This appears to consist of nothing more than a rostral extension of the superior labials, which meet at the tip of the upper jaw to form a median enlargement, which in some forms (e.g. *Oligodon cyclurus*, *Coluber fasciolatus*) appears on dissection to have become separated from the superior labial on either side. Its ducts open inside the labial margin external to the anterior teeth.

(3) *The parotid gland of the Aglypha and the Opisthoglypha.*

The term parotid gland is used here to distinguish this structure from the venom gland of Viperidae and Elapidae, and is applied to any differentiation of the hind part of the superior labial in the Aglypha and Opisthoglypha. The stages in its evolution have been suggested by both Phisalix (1922) and Sarkar (1923), and we can confirm their observations.

The first stage in the evolution of this gland is represented by a slight enlargement of the posterior part of the superior labial, whose ducts, passing to open externally to the posterior maxillary teeth, also show an increase in size. This stage is seen in some aglyphous colubrids, such as *Thamnophis sirtalis* and some species of *Natrix* (fig. 5).* Often the macroscopic appearance of this region of the superior labial shows a difference in coloration or in superficial pattern from that over the rest of the gland (e.g. *Ptyas mucosus*, Pl. **5**, fig. L).

From this initial stage, every step in the elaboration of the parotid can be demonstrated among colubrine snakes. There is a gradual increase in its size and a more apparent distinctness in its superficial pattern until finally, in certain forms, the gland, though still embedded in the superior labial, has acquired its own fascial sheath and can be dissected out as a separate structure. At the same time, ducts for the discharge of its secretion to the posterior teeth have appeared, either two or three convergent channels or a single duct opening into a pocket lateral to the base of the teeth. When this stage is associated with the grooving of the posterior teeth, the opisthoglyph condition is said to have been reached. A drawing of the medial aspect of the parotid gland showing its duct in the opisthoglyph *Boiga cynodon* is given in fig. **6**.

* Phisalix figures a differentiated parotid in *Natrix natrix* but we were unable to observe it on macroscopic examination of several specimens.

The evolution of the parotid gland from the superior labial is intimately associated with changes occurring in the posterior maxillary teeth, two or three of which become increased in size, and acquire grooves down which the secretion can pass into the wound. These changes in the glands and teeth, however, do not always proceed *pari passu*. In *Ptyas*, for instance, the posterior part of the superior labial gland shows macroscopic differentiation in pattern, but there is no enlargement of the teeth. The converse is illustrated by the example of three aglyphous colubrids, *Ahaetulla caudolineata*, *Oligodon cyclurus* and *Macropisthodon rhodomelas*, which may be considered as a series; none of these snakes shows any macroscopically visible differentiation of the gland. In *Ahaetulla* there is no enlargement of the posterior teeth; in *Oligodon* they are considerably enlarged, while in *Macropisthodon* they are enormous.

In general, the differentiation of the gland precedes the grooving of the teeth, but not always their enlargement. Here, again, however, lack of correlation may

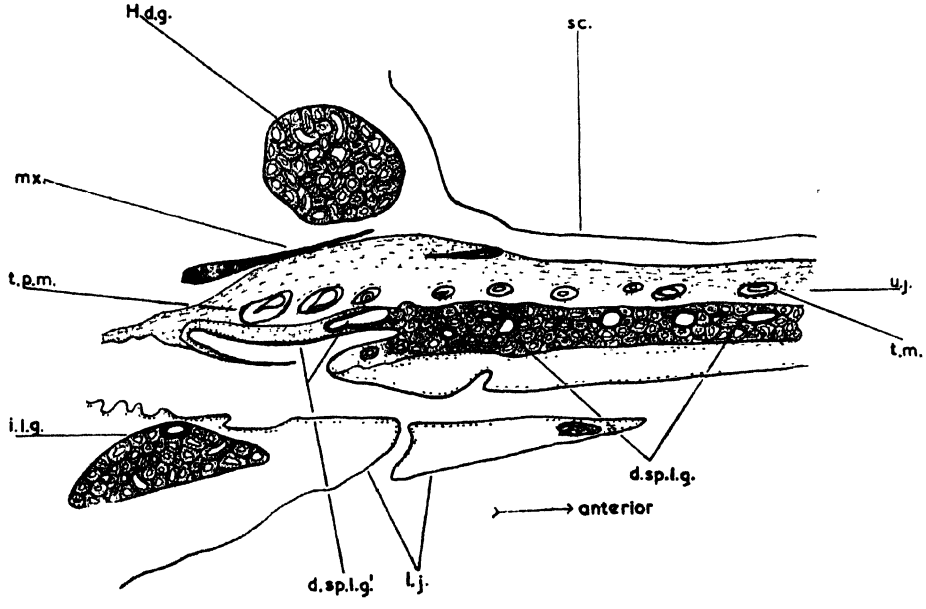


FIG. 5. *Thamnophis sirtalis*. Paramedian section through jaws showing enlarged posterior ducts of superior labial gland.

occur. In *Macropisthodon*, for instance, the posterior teeth are very large, but there are no grooves, while in *Herpeton* the grooves are distinct, though the posterior teeth are scarcely enlarged.

An interesting feature of these changes is the very considerable variation which may occur in species which are relatively closely related, a phenomenon which is clearly shown among the genus *Natrix*. In *Natrix natrix* there is a gradual enlargement of the maxillary teeth from the front backwards; in *N. stolata* and *N. subminiata helleri* the last two teeth are abruptly enlarged. In all three species the superior labial gland is well developed and enlarged posteriorly, but whereas in *N. natrix* and *N. stolata* no separate parotid is evident, in *N. subminiata helleri* this gland is clearly differentiated as a separate entity, and possesses a single large duct conveying its secretion to the posterior teeth.

Laboratory experiments by Alcock and Rogers (1902) have shown that the secretion of the differentiated parotid gland, both in the Aglypha and the Opisthoglypha, is toxic to small vertebrates, and this has been subsequently confirmed by Phisalix. Alcock and Rogers found the effects of the secretion to vary greatly in different species, but in general the Opisthoglyphs were more toxic than the Aglyphs, as might be expected. With some species, the secretion was toxic for lizards but not for mammals. It is known that the saliva of many Opisthoglyphs such as *Coelopeltis*, *Tarbophis*, *Trimorphodon*, *Dryophis* and *Dispholidus* is toxic to their normal prey; Green (1903) and also McCann (1934) have seen the Common Green Whip Snake (*Dryophis nasutus*) of the Oriental region catch lizards by the neck and hold them until they were dead some minutes later. Death in these cases may have been due to strangulation, but the signs observed were chiefly those of paralysis. On the other hand, when this snake attacks warm-blooded vertebrates it usually kills them by constriction, and *Chrysopelea* and many species of *Boiga* do the same. All these snakes have well-developed parotid glands and grooved teeth. There are many records of people having been bitten by opisthoglyphous snakes, and in the vast majority of cases no effects at all were observed. Occasionally the bite was followed by some pain and swelling which quickly passed off. Two factors contribute to this: the low toxicity of the venom for man, and the posterior position of the fangs, which makes it difficult to bring them into action. In fact, with some snakes such as *Macropisthodon*, *Tomodon* and *Dispholidus* the enormous length of the fangs and their direction straight backwards into the mouth, makes it hard to understand how they can be engaged at all. *Dispholidus*, however, is said to overcome this difficulty by having an enormous gape. All who have handled and been bitten by snakes with large posterior fangs will have observed how they hang on, and by chewing movements endeavour to bring their posterior teeth into action.

The little that is known of the effects of the venom of the parotid in the Opisthoglypha indicates that its main action is on the nervous system. In this respect it approximates rather to the venom of the Elapidae than to that of the Viperidae, the predominating action of which is haemolytic. The venom of the well-known Boomslang (*Dispholidus typus*) appears to be considerably more toxic than that of other opisthoglyphs; large mammals such as dogs and monkeys may succumb to it in less than an hour. In its physiological action it is said to approach nearer to the viperine type of venom.

(4) *The Venom glands of Viperidae and Elapidae.*

The general appearance and relations of the viperine venom glands are well known (see Boulenger, 1913). In most vipers they are prominent pyriform structures invested in a thick fibrous capsule and situated in the temporal region on either side, producing the characteristic swollen contours of the viperine head. Fibres from the adductor mandibulae muscle complex are inserted into the investing sheath and serve to compress the gland and expel the secretion when the snake strikes and the fangs, erected by the movement of the maxilla, are inserted into the prey. In *Causus rhombeatus* and other members of its genus the venom gland has undergone a remarkable backward prolongation and extends along each side of the neck for some distance. A parallel modification is found in the elapid *Maticora* (=*Doliophis*), but here the gland is prolonged even further backwards, and ends just in front of the heart.

The venom duct in vipers arises from the anterior part of the venom gland and passes forwards beneath the eye, and then bends downwards, medial to the superior labial gland, to open round the grooved base of the poison fang (fig. 7). The actual relations of the terminal part of the duct to the base of the fang and reserve fang are shown in fig. 8, a drawing of a cross-section of the fang-bearing part of the maxilla in *Vipera russelli*. The venom duct is seen cut twice as it bends downwards

describing a semicircle, which in life is partially straightened as the fang is erected. The terminal part of the duct opens out around the anterior part of the fang, which is grooved; further down the fang the edges of this groove unite to form a closed channel. An extension from the lower part of the duct passes outwards to open around the base of the reserve fang in a similar manner. It will be seen that the termination of the duct does not form a tight sleeve around the fang base, and that a considerable space exists between the sides of the fang lateral to the groove and the wall of the duct through which it might be supposed that much of the venom would trickle into the mouth. In fact, it is well known that the venom may be forcibly ejected several inches from the fang by a striking snake. It is possible,

FIG. 6.

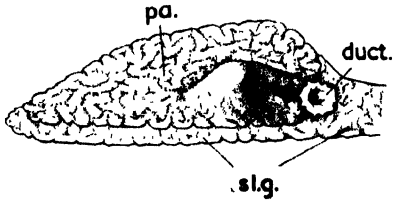


FIG. 7.

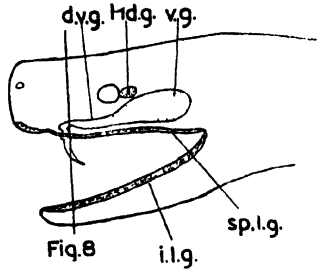


FIG. 8.

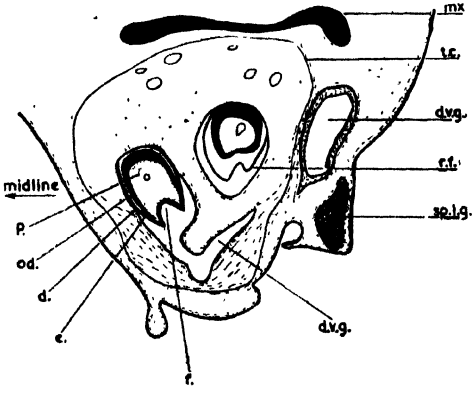


FIG. 9.

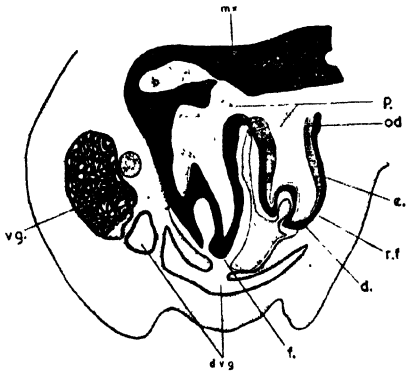


FIG. 6.—*Boiga cynodon.* Medial aspect of parotid gland showing its duct.
FIG. 7.—*Vipera russelli.* Drawing of head showing plane of section in fig. 8.
FIG. 8.—*Vipera russelli.* Transverse section through fang region, showing relationship of duct of venom gland to the fang.
FIG. 9.—*Bungarus fasciatus.* Transverse section through fang region. (Right of fig. towards midline.)

therefore, that there may be some physiological contraction of the lower part of the venom duct, forming a temporary closed system with the groove, and allowing the fang to act as a hypodermic syringe. The frequent shedding of the fangs would in any case appear to preclude the development of a more intimate structural connection between the base of the fang and its duct, as was pointed out by West (1898).

Boulenger (1896) has suggested a hypothetical origin of the viperine fang from the opisthoglyphous dentition by supposing a progressive forward migration of the enlarged posterior maxillary teeth combined with a relative shortening of the maxilla, and disappearance of the anterior maxillary teeth. Following this view the evolution of the viperine venom gland from the opisthoglyph parotid could be explained by an increasing differentiation of the parotid gland which loses all connection with the superior labial, while its duct is carried forward by the migration of the enlarged posterior teeth. The embryological researches of Martin (1899), however, do not confirm this view, since, according to this worker, the venom glands arise from separate epithelial buds to those which give rise to the labial glands.

The venom apparatus of the Elapidae (cobras, kraits, coral snakes and sea snakes) shows certain differences from the viperine structure, which, however, it resembles in general. In these forms the fangs are relatively smaller, are derived rom the anterior series of maxillary teeth, and are immovably fixed in position. In *Bungarus fasciatus*, serial sections of which were available, the body of the venom gland extends relatively further forward than in vipers, and its duct is correspondingly shorter. The anterior portion of the venom gland and its duct were in very close relationship to the superior labial, which was penetrated by the duct as it passed medially to reach the poison fangs (fig. 9). The arrangement of the fang base and termination of the duct was very similar to that observed in *Vipera russelli*. Dissection of *Naja naja* (Pl. 5, fig. N) and accounts by West (1895) and Phisalix (1922) suggest that the condition in other proteroglyphs is very similar.

There are no indications as to how the venom apparatus of these snakes may have been evolved; possibly the anterior part of the superior labial may have become modified to give rise to the venom gland, but no intermediate stages are found among living forms, and no embryological investigations appear to have been recorded.

(5) *The anterior temporal gland.*

This gland was first recorded by Phisalix (1922), who figures it in *Ilysia scytale*, *Eryx johni* and *Platyplecturus* (? sp.), and lists it as present in *Ungalia maculata*, *Eryx conicus*, *Rhinophis trevelyanus*, *Uropeltis nigra*, *U. pulneyensis* and *Plecturus perottetti*. It is also figured by Haas (1930) in *Silybura* (*Uropeltis*) *brevis* and *Xenopeltis unicolor*. Phisalix observes in her monograph (p. 395, vol. 2) "that in the Ilysidae, Boidae and Uropeltidae there exists a gland more deeply situated than the parotid and which our experience shows to be venomous. It is lodged in a depression in the anterior mandibular muscle, and extends forwards to the posterior end of the maxilla." She terms this gland the anterior temporal, but gives no account of the distribution of its ducts.

We were able to find this gland by dissection in *Uropeltis ceylonicus*, *Cylindrophis rufus*, and also in certain aglyphous Colubrids (*Coluber fasciolatus*, *Ptyas mucosus*, and some members of the genera *Lytorhynchus* and *Elaphe*). It is doubtless present in many other snakes, but it is often difficult to demonstrate by dissection on account of its small size. It is easily overlooked in a superficial dissection, since it is partly overlapped by the posterior end of the superior labial gland, and by the ligamentum zygomaticum, a strong fibrous band which passes forwards from the quadrate bone to be inserted into the capsule of the superior labial and the tissues around the posterior end of the maxilla. The distribution of the anterior temporal, at any rate as a well-developed structure, appears to vary considerably in members of the same genus. For instance, the gland is well developed in *Coluber fasciolatus* from N.W. India, but could not be distinguished on dissection in *Coluber gemonensis* from Cyprus. In *Xenopeltis* and certain Boids there appeared to be small saccular or nodular structures in the region of the junction of the upper and lower jaws, but without microscopic examination it was impossible to say whether they

were glandular in nature and what was their relationship to the posterior end of the superior labial. In certain lizards (e.g. *Anguis*) and snakes (e.g. *Trachyboa*), of which serial sections were available, small glands were found to discharge beneath the posterior labial scales at the junction of the jaws, and appeared to represent elements of the labial glands prolonged backwards behind the jaw junction. It is possible that the anterior temporal has been evolved from such structures, and it is clear that microscopic examination of sections provides the only satisfactory criteria for determining the existence of the anterior temporal gland as a distinct entity.

Of the forms in which a distinct anterior temporal can be demonstrated by dissection, serial sections of *Cylindrophis rufus* and *Coluber fasciolatus* were available. In both these widely separate types the form and relations of the gland was essentially similar, though the structure is considerably more obvious on dissection in *Coluber*. Anteriorly, the gland lies between the extra-orbital part of the Harderian and the superior labial, and is prolonged backwards behind the superior labial, from which it is separated by a layer of connective tissue (fig. 10). In both forms the posterior

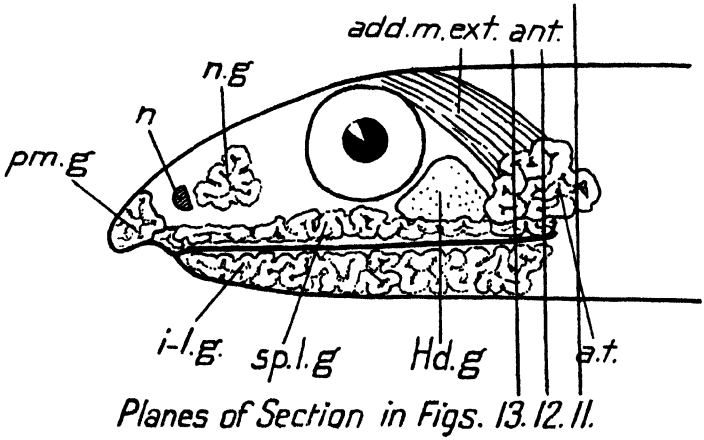


FIG. 10.—*Coluber fasciolatus*.
Drawing of head showing anterior temporal gland and planes of section in figs. 11–13.

part of the gland divided into an upper portion which terminated in the tempora region, and a lower portion which passed downwards and gave origin to the duct system. In *Cylindrophis* the single duct is long and tortuous, and opens on to the surface of the head beneath the last labial scale, just behind the junction of the upper and lower jaws. In *Coluber* there are several short ducts which discharge directly downwards to open beneath the scale in a similar manner (figs. 11, 12, 13).

The function of this interesting gland is obscure. Although it does not discharge directly into the mouth, it seems likely that the bulk of its secretion would pass forwards into the mouth when the jaws are widely open and would reach the surface of the prey when the snake was feeding. The gland can therefore probably be regarded as having a salivary function; unfortunately Phisalix does not cite her evidence when she states that its secretion is venomous. The possibility that it may function as an integumentary gland comparable with the small skin glands in *Typhlops* or the vertebral (=nucho-dorsal) glands described by Smith (1938) in certain species of *Natrix* and *Macropisthodon* cannot be entirely eliminated.

In her monograph (p. 397) Phisalix describes a gland in *Typhlops punctatus* lying in the temporal region. She regards this as distinct from the anterior temporal,

which is not found in *Typhlops*, and terms it the "temporo-medial gland." From examination of her figure and comparison with a series of transverse sections through the head of *T. diardi*, it seems highly probable that this gland is nothing more than a posterior prolongation of the inferior labial, which extends backwards and upwards into the temporal region, and comes into relationship with the Harderian gland (figs. 14–18). A similar prolongation of the superior labial gland into the temporal region has been observed by Radovanovic (1935) in *Rhinophis*.

(6) *The Harderian gland.*

This gland, variously described as the Harderian gland, lachrymal gland, or great orbital gland, was well known to the earlier workers, but the remarkable relationships of its duct system with the sub-brillar space (closed conjunctival space)

FIG. 11 FIG. 12 FIG. 13

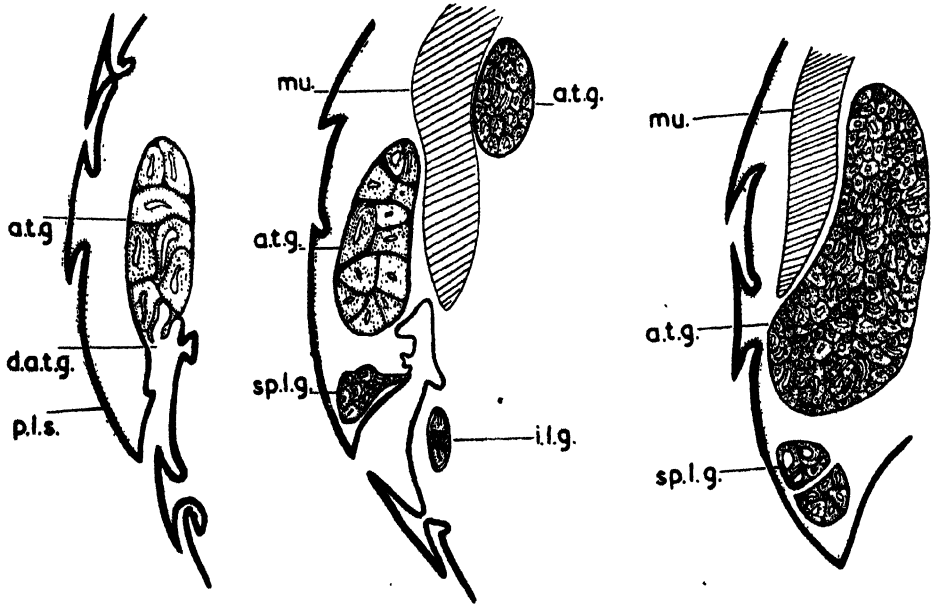


FIG. 11.—*Coluber fasciolatus.* Transverse section through lateral part of temporal region showing ducts of anterior temporal gland discharging beneath posterior labial scale.
FIG. 12.—*Coluber fasciolatus.* As fig. 11, but a few sections further forward, showing division of posterior part of anterior temporal gland.
FIG. 13.—*Coluber fasciolatus.* As fig. 12, but a few sections further forward, showing relationship of anterior temporal to superior labial gland.

and upper end of the lachrymal duct were not described correctly until the work of Born (1876–83; see Franz's account in the handbook by Bolk and others). The gland has recently been described by Schwarz-Karsten (1937) in a number of lizards and *Natrix natrix*, by Bellairs (1942) in *Viperia berus*, and by Walls (1942) in his general account of the vertebrate eye. A detailed study of this gland in the Squamata by Bellairs and Boyd is in preparation, and the following account is in general terms only.

The gland is present in all lizards and snakes, as well as in many other reptiles, birds and mammals. In lizards, where a lachrymal gland also may be present,

it lies at the anterior pole of the eyeball and discharges typically into the conjunctival space deep to the nictitating membrane. In snakes, where the lachrymal gland is absent, the Harderian is always well developed, and in some forms (e.g. with reduced eyes, such as *Typhlops* and *Rhinophis*) it is relatively enormous, completely surrounding the eyeball and optic nerve. The body of the gland lies behind the

FIG. 14.

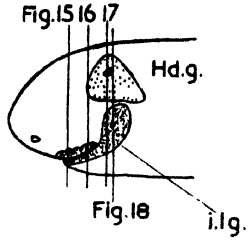


FIG. 15.

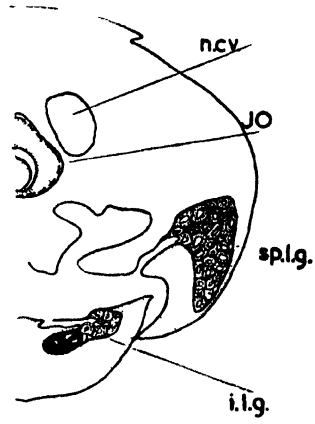


FIG. 16.

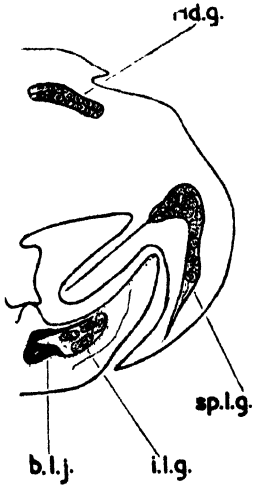


FIG. 17.

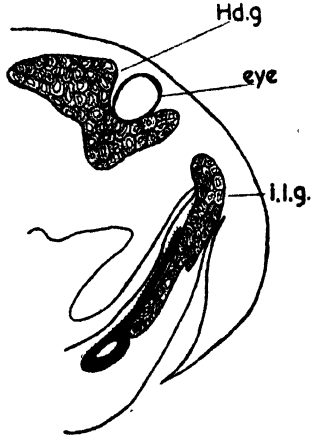


FIG. 18.

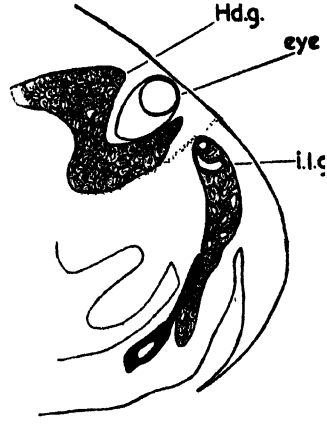


FIG. 14.—*Typhlops diardi.* Drawing of head showing posterior extension of inferior labial gland into temporal region and planes of section in figs. 15–18.
FIGS. 15–18.—*Typhlops diardi.* Series of transverse sections passing progressively backwards, showing extension of inferior labial gland into temporal region.

orbit and is readily visible when the skin has been removed. This part of the gland is highly variable in size, being very small in *Dryophis* (Pl. 5, fig. J) and very large and prolonged backwards for some distance in the egg-eaters, *Dasypeltis* (Pl. 4, fig. E) and *Elachistodon*. The gland passes forward medial to the post-orbital

bone, when this is present, and runs anteriorly beneath (in some cases surrounding) the optic nerve in the medial wall of the orbit as a flattened band-like structure. Its duct arises in the anterior part of the orbit and in most snakes (e.g. Colubridae, Elapidae, Viperidae) it discharges directly into the upper part of the lachrymal duct, which passes forwards and downwards to open into the lower part of the duct of Jacobson's organ (fig. 19). In such forms no ducts from the gland communicate directly with the sub-brillar space, but this does, however, communicate with the lachrymal duct by a very fine channel which may perhaps disappear entirely in certain burrowing forms (e.g. *Rhinophis*). It was the exiguity of this channel in *Vipera berus* that led one of us (Bellairs, 1942) to the erroneous conclusion that in this form the sub-brillar space was a closed cavity, and that it was the duct of the Harderian gland, and not the lachrymal duct, that opened in the neighbourhood of Jacobson's Organ. A series of drawings of microscopic sections showing the

FIG. 19.

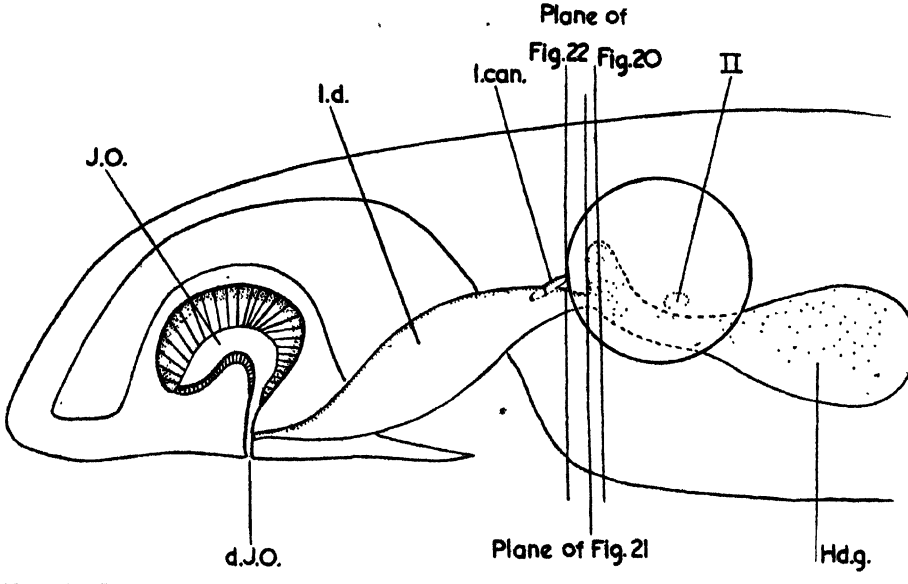


FIG. 19.—Diagram showing relation of Harderian gland to orbit, lachrymal duct and sub-brillar space, and planes of section in figs. 20, 21, 22. Based on *Natrix natrix*. (Not to scale.)

relationship of the duct of the Harderian gland to the lachrymal duct, and of the latter to the sub-brillar space in *Natrix natrix* is given in figs. 20, 21, 22.

In certain primitive snakes (e.g. *Cylindrophis*, *Boa*), however, the Harderian gland communicates directly with the sub-brillar space by a number of separate ductules, while its main duct discharges into the upper end of the lachrymal duct, which has a relatively wide communication with the sub-brillar space. The functional and phylogenetic aspects of these relationships will be discussed in detail in the separate paper by Bellairs and Boyd.

(7) *The inferior labial glands.*

These glands correspond in position with the superior labials, lying along the margins of the lower jaw, and opening similarly by a number of ducts lateral to the teeth (fig. 24). It is interesting to note that they are better developed than the

FIG. 20.

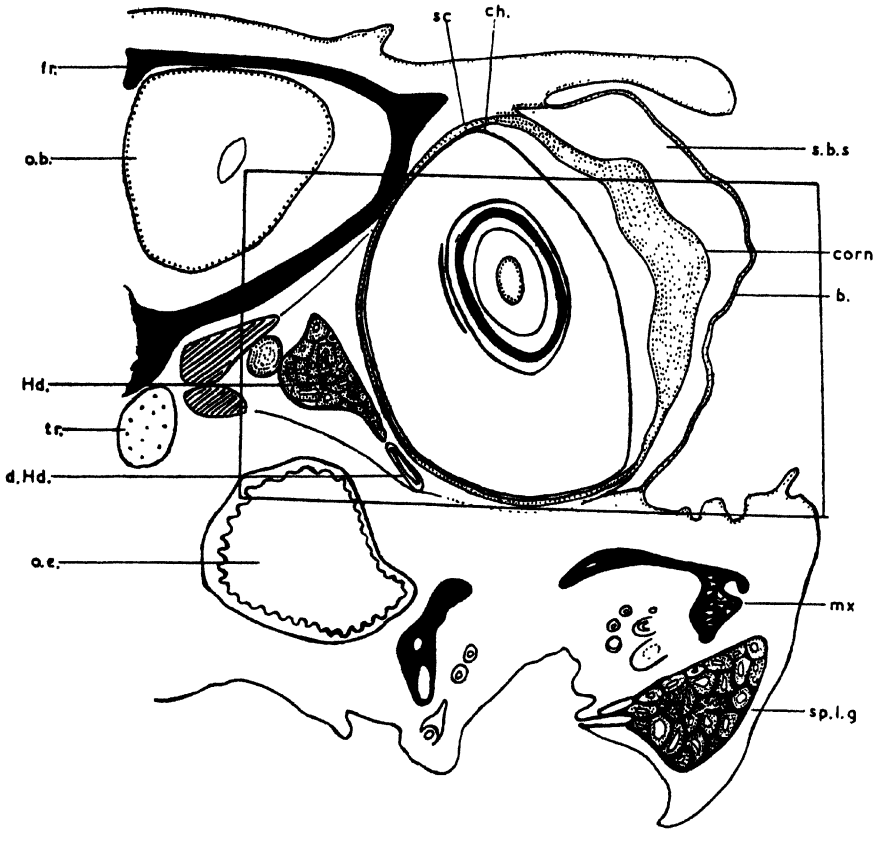


FIG. 21.

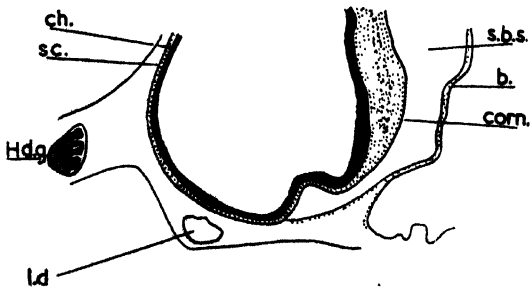


FIG. 22.

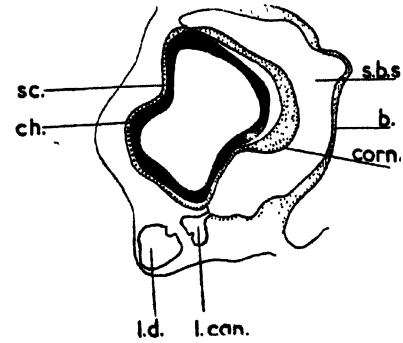


FIG. 20.—*Natrix natrix.* Transverse section through front of eye showing duct of Harderian gland discharging into upper end of lachrymal duct.

FIG. 21.—*Natrix natrix.* As fig. 20 (area in rectangle), but a few sections further forward.

FIG. 22.—*Natrix natrix.* As fig. 21, but a few sections further forward, showing connection between sub-brillar space and lachrymal duct.

For corn. in figs. 20-22 *read* sc.

superior labials in most primitive snakes (e.g. *Xenopeltis*) and in most lizards. It is from the inferior, and not the superior, labial glands, that the venom glands of the poisonous lizard, *Heloderma*, have been developed.

(8) *The nasal glands.*

These were present in all the snakes examined, though their size was very variable, being small in *Vipera*, and very large in *Xenopeltis*. The body of the gland lies beneath the skin behind the nostril on each side, and posteriorly the gland passes inwards and is incorporated into the nasal concha, where it lies, completely surrounded by cartilage, within the nasal cavity. Its ducts could not be demonstrated by dissection, but the gland was observed in microscopical sections (*Xenopeltis*,

FIG. 23.

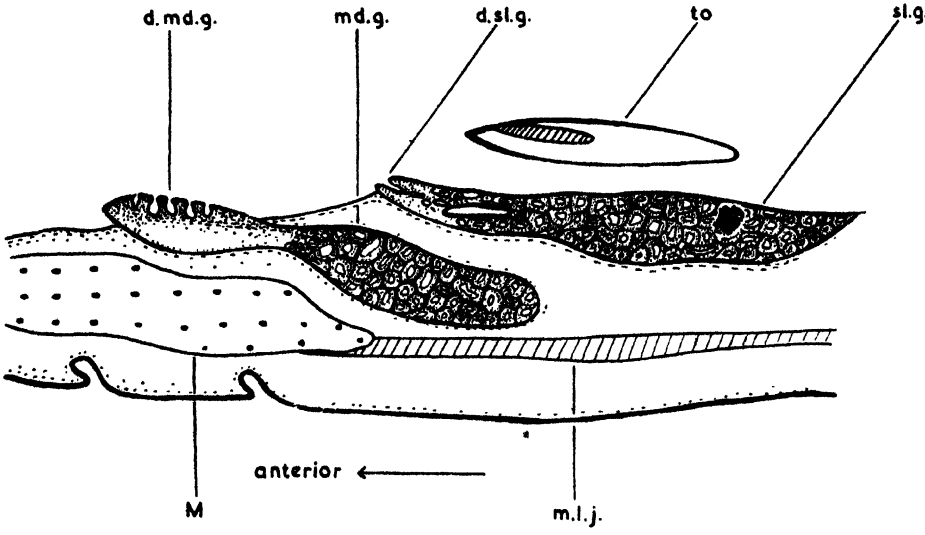


FIG. 23.—*Thamnophis sirtalis.*
Paramedian section showing glands at lower jaw and their ducts.

Cylindrophis rufus, *Typhlops diardi*, *Boa constrictor*, *Thamnophis sirtalis*, *Vipera berus* and others) to discharge by one or more ducts into the posterior aspect of the groove of the nostril or into the adjoining part of the nasal cavity (figs. 1–4).

(9–10) *The mandibular and sublingual glands.*

The glands of the lower jaw consist of a pair of mandibular glands (lateral mandibular glands of Fahrenholz's account), and a single median sublingual gland which Fahrenholz regards as representing the fused medial mandibular glands of some lizards.

The mandibular glands are pear-shaped structures lying one on either side of the midline at the front of the lower jaw and directed obliquely inwards so that their anterior ends, which bear the ducts, nearly meet in the midline (figs. 24 and 27). Each gland discharges by a series of short ducts (six in number in *Thamnophis*) which are separated by short thick papillae (fig. 23). The posterior parts of the glands lie deeper in the tissues of the jaw, and are closely surrounded by muscles.

FIG. 24.

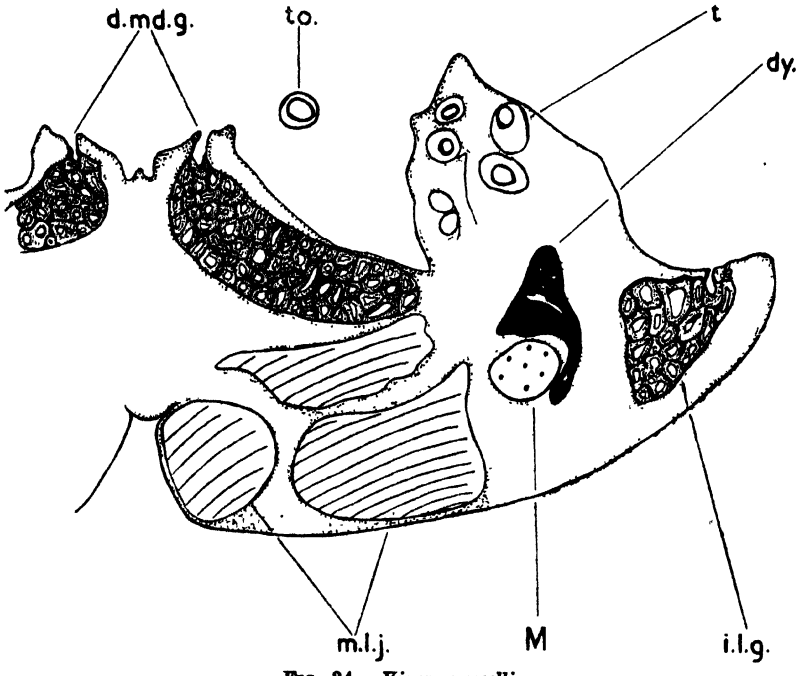


FIG. 24.—*Vipera russelli.*
Transverse section through lower jaw showing mandibular and inferior labial glands.

FIG. 25.

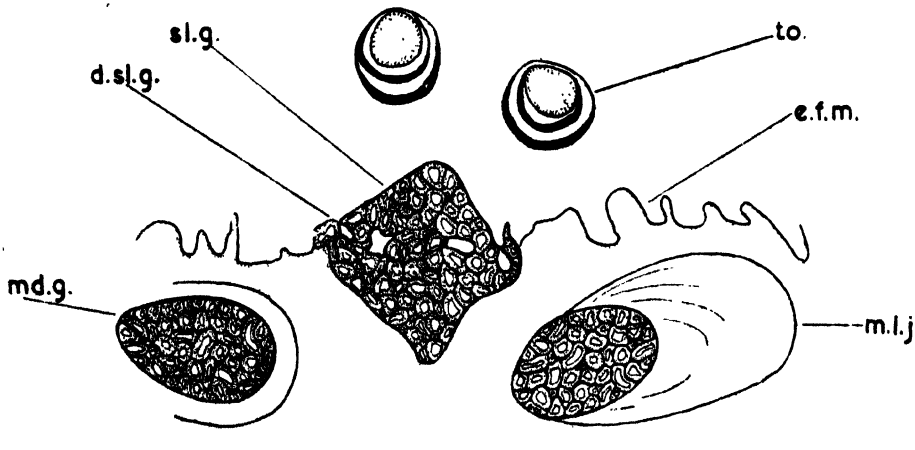


FIG. 25.—*Vipera russelli.*
As fig. 24, but further back, showing sublingual gland.

The sublingual gland is an elongated median structure closely applied to the floor of the tongue sheath, and extending from the level of the hinder parts of the mandibular glands to a region well behind the epiglottis (figs. 23–27). West (1898) observed this gland in some of the snakes which he examined, but he does not state the species. He describes it as discharging by numerous ducts into the sheath of the tongue, but in most of the species examined microscopically by us the ducts discharged at a level well anterior to the tongue sheath, although some of the secretion would doubtless be carried back into this structure by the movements of the tongue. The ducts appeared to be most numerous at about the level of the posterior ends of the mandibular glands, and were arranged in a longitudinal series on either side of the midline (figs. 23 and 25). Further back the gland was separated from the tongue sheath by a layer of connective-tissue, and ducts perforating this were observed only in *Bungarus* (fig. 26). In some species, however (*Xenopeltis*, *Cylindrophis*), the tongue sheath was lined with secreting epithelium, or possessed a few small isolated glands opening into it (*Boa*). The sublingual gland could not be identified microscopically in *Xenopeltis*, *Cylindrophis*, *Typhlops* or *Trachyboa*, and was poorly developed in *Boa constrictor*.

FIG. 26.

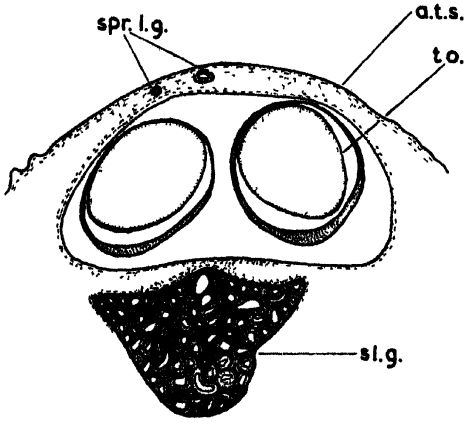


FIG. 27.

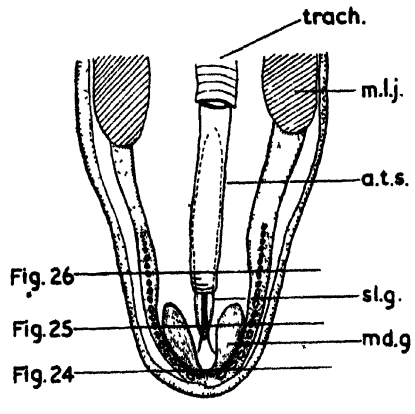


FIG. 26.—*Vipera russelli*. As fig. 25, but further back, showing relation of sublingual gland to tongue sheath.

FIG. 27.—*Vipera russelli*. Drawing of dissection of glands of lower jaw from above after removal of epiglottis and trachea. Planes of section in figs. 24, 25, 26 are shown.

The existence of the small paired "supralingual glands" described by Bisogni (1897) in vipers was confirmed in *V. berus* and *V. russelli*, where they were seen to lie on the dorsal aspect of the tongue sheath at about the level of the epiglottis (fig. 26). Since their ducts open into the tongue sheath, however, and not on to the dorsal surface of the epiglottis and trachea, they can hardly be regarded as homologous with the crico-arytenoid glands of lizards, as is suggested in Bolk's handbook.

LIST OF MATERIAL EXAMINED.

(1) *By microscopic examination of serial sections.*

Family.	*Genus and species.*	*Glands examined.*
Xenopeltidae ..	*X. unicolor*	nasal, Harderian, mandibular.
Ilysiidae	*Cylindrophis rufus*....	nasal, Harderian, mandibular, labial, anterior temporal.

Typhlopidae ..	*T. diardi*	nasal, Harderian, mandibular, labial, anterior temporal.
Boidae	*Boa constrictor*	nasal, Harderian, mandibular, sublingual.
	Trachyboa boulengeri .	nasal, Harderian, mandibular, labial.
Colubridae	*Natrix natrix*	Harderian.
	Thamnophis sirtalis...	nasal, Harderian, mandibular, sublingual, labial.
	Coluber fasciolatus ...	anterior temporal.
Viperidae	*V. berus*	nasal, Harderian, mandibular, sublingual, labial, venom gland, supralingual.
	V. russelli	
Elapidae	*Bungarus fasciatus* ...	nasal, Harderian, labial, venom gland.

(2) *Spirit specimens dissected.*

BOIDAE.

Boa constrictor, Enygrus asper, E. australis, Epicrates cenchris, Corallus cookei, Nardoa gilberti, Eunectes murinus, Tropidophis melanurus, Trachyboa gularis, Lichanura trivirgatus, Boleria multicarinata, Charina bottae, Caesarea dussumieri, Eryx jaculus, Python spilotes, Calabaria reinhardti.

TYPHLOPIDAE.

Typhlops diardi, T. punctatus.

UROPELTIDAE.

Uropeltis ceylanicus.

ILYSIIDAE.

Ilysia scytale.

XENOPELTIDAE.

Xenopeltis unicolor.

COLUBRIDAE.

Pareas carinatus, Acrochordus javanicus, A. granulatus, Dasypeltis scaber, Elachistodon westermanni, Elaphe radiata, Ahaetulla caudolineata, Oligodon cyclurus, Macropisthodon rhodomelas, Coluber fasciolatus, C. gemonensis, Ptyas mucosus, Natrix natrix, N. stolata, N. subminiata, Boiga dendrophila, Psammophis sibilans, Dryophis nasutus, Chrysopelea ornata, Cerberus rhynchops, Dispholidus typus.

VIPERIDAE.

Vipera berus, V. russelli, Trimeresurus popeorum, T. erythrurus, Crotalus terrificus, Causus rhombeatus.

ELAPIDAE.

Naja naja, Bungarus caeruleus, Dendraspis angusticeps, Notechis scutatus, Denisonia superba.

HYDROPHIIDAE.

Lapemis hardwickii.

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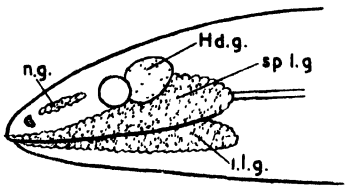

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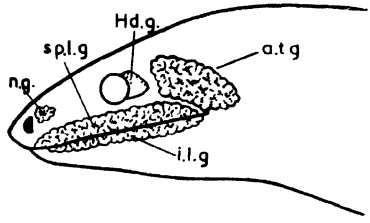

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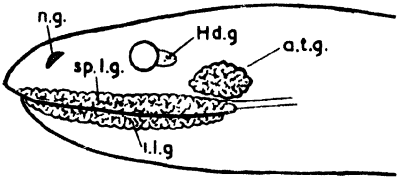

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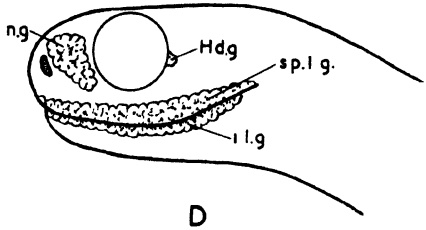

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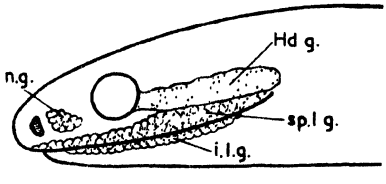

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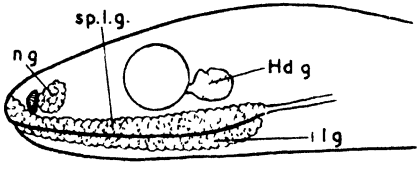

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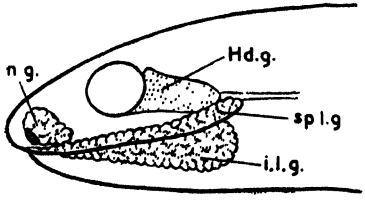

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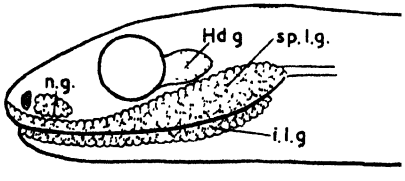
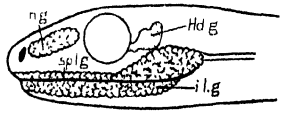


H

A.—*Ilysia scytale.*
C.—*Eryx jaculus.*
E.—*Dasypeltis scabra.*
G.—*Macropisthodon rhodomelas.*

B.—*Uropeltis ceylanicus.*
D.—*Pareas carinatus.*
F.—*Ahaetulla caudolineata.*
H.—*Natrix natrix.*



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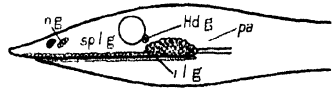

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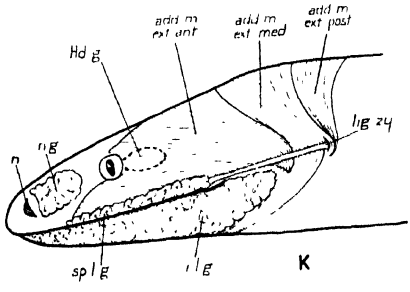

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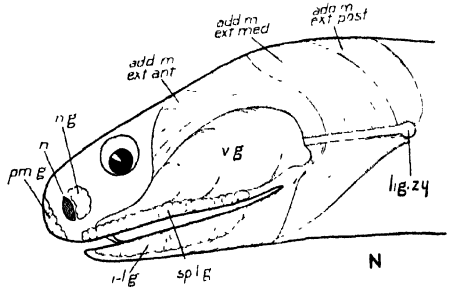

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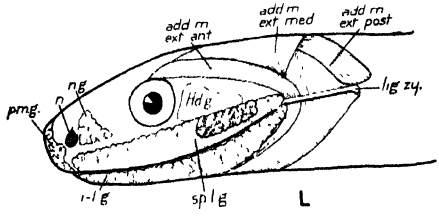

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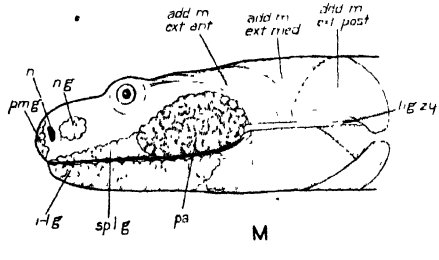

M

I.—*Psammophis sibilans.*
K.—*Xenopeltis unicolor.*
M.—*Cerberus rhynchops.*

J.—*Dryophis nasutus.*
L.—*Ptyas mucosus.*
N.—*Naja naja.*

Contributions to the study of some African mammals—VI. Notes on the interior of the skull in Lion, Leopard, and Cheetah.

By A TINDELL HOPWOOD, D.Sc., F.L.S., Department of Geology, British Museum.

(PLATES 6 & 7, and 2 Text-figures)

[Read 21 November 1946]

Although many authors have described skulls of one or other of these three species, and none better than Dawkins and Sandford when dealing with the Cave Lion nearly eighty years ago, very little has been written about the inside of the skull. The latest author, Haltenorth, in a very long and detailed paper on the relationships of the great cats expressly says that he was unable to dissect the skulls. This is the more unfortunate in that he had at his disposal a far greater mass of material than have most authors; of the three species here dealt with, he had 124 skulls of Lion, 450 of Leopard, of which all but 72 had been collected in Tanganyika Territory, and 47 African Cheetah. In contrast I had one Lion, two Leopard, and a Cheetah, all unlocalized and bought for a few pence here and there as the opportunity offered. Through the kindness of Mr. M. A. C. Hinton, F.R.S., who gave me permission to section them, I was able to add two others of each species preserved in the Department of Zoology of the British Museum.

I. MEASUREMENTS.

The following measurements in millimetres are those of a male of each species shot in East Africa; the Leopard and Cheetah were chosen because their basal lengths are approximately equal. The figures in italics are the proportions when the basal length is taken as 100.

	LION	LEOPARD	CHEETAH
Basal length	282	153	149
	100	*100*	*100*
Bizygomatic width	221	117	134
	78·3	*76·5*	*90*
Length of palate	136	77	68
	48·2	*50·4*	*45·6*
Width of palate outside P4	123	74	73
	43·6	*48·4*	*49*
Width of brain-case	94	68	69
	33·3	*44·5*	*46·3*
Interorbital width	70	34	41
	24·8	*22·4*	*27·5*
Width of post-orbital constriction	61	43	35
	21·6	*28·1*	*36·9*

The most significant of these dimensions are the width of the brain-case and the post-orbital constriction. From the former one would deduce that the Lion has a relatively smaller brain than either of the other species, and from the latter that it is more primitive; both these deductions are supported by the facts.

II. AIR SINUSES.

The sinuses of the Cheetah are much greater than those of the Leopard. The largest is the frontal sinus (2^1 of Paulli's notation). In the Leopard this usually forms a single chamber in the posterior part of the frontal bone, and is strengthened

here and there by septa which project inwards from the periphery of the cavity. The sinus opens into the olfactory chamber of the nose by means of a small oval foramen between the basal lamellae of the first and second ectoturbinals, and the lateral lamina of the latter may extend backwards through the foramen into the sinus.

In all these features the Leopard agrees with the Lion and Cat (Paulli, 1900 ; Leopard not described), but the skull of an adult female (basal length 160 mm.) shot at Muhambwe, S. Kigoma District, Tanganyika Territory (regd. 36.2.28.20. B.M. Zool. Dept.), shows an interesting individual variation. The frontal sinus of this specimen is very small ; it occupies that part of the bone which is medial to the post-orbital process, is posterior to the line joining the tips of those processes and is anterior to the semi-circular line (linea semicirc. oss. front.). The remainder of the posterior moiety of the frontal, normally occupied by an extended sinus, is filled with cancellous tissue, of which the cells communicate with the sinus proper by numerous irregular foramina.

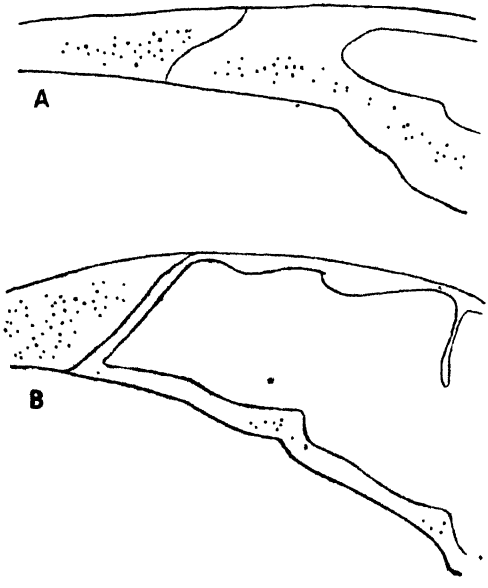

FIG. 1.—Median longitudinal sections through the fronto-parietal suture of young (A) and old (B) adult Cheetahs. The outer table of the parietal projects beyond the inner and in the old animal the frontal sinus extends backward to the limit of the frontal bone. It does not invade the parietal.

According to Paulli (*op. cit.*) the frontal sinus of the Cheetah is large and extends throughout the hinder-half of the bone into the anterior portion of the parietal. A specimen, probably from Angola (regd. 26.6.4.4.), chosen because of its size (basal length, 163 mm.), agreed with the other specimens examined in having sinuses co-extensive with the frontal bones, but not invading the parietals. This specimen affords a possible explanation of Paulli's statement. It will be seen from Fig. 1 that the anterior margin of the parietal and the posterior margin of the frontal are bevelled in such a way that the outer table of the parietal projects beyond its inner table and actually lies over part of the frontal sinus. Paulli opened the sinus from above by means of a chisel, a method which when applied to an old skull with the sutures almost obliterated would be very unlikely to reveal the fact that the posterior wall of the sinus is composed of two laminae, and that the parietal is excluded from

the boundaries of the cavity. The foramen between the first and second ectoturbinals, by which the sinus and nasal cavity communicate, is a rather irregular oval and is very large; it measures approximately 10×4·5 mm. The septa are much better developed than they were in the Leopards examined.

One specimen of a Cheetah was peculiar because of the marked asymmetry of the frontal sinuses. That on the left occupied the whole of the frontal bone, but that on the right was relatively small. It is confined to the lateral moiety of the posterior half of the bone. Between the medial wall of the sinus and the sagittal suture is a very big cavity which communicates freely with the olfactory chamber, of which it forms a part, and extends back to the coronal suture; it originally contained a backward extension of the first ectoturbinal. This cavity opens into the sinus proper by means of a foramen in its posterior wall.

The proximal portions of the nasal bones of both Leopard and Cheetah contain a large cavity, greater in the latter species, which is freely open behind into the nasal cavity. This nasal sinus often contains an anterior extension of the first endoturbinal. I found no such cavity in the Lion.

The sphenoidal sinus (sinus IV of Paulli) is very much larger in the Cheetah than in the Leopard. Not only does it take up more room in the presphenoid, but it extends back into the basisphenoid and outwards into the alisphenoid. It abuts directly against the hypophyseal fossa, from which it is separated by a thin plate of bone. In the Leopard the sinus is much smaller and does not extend so far back; there is an appreciable extent of ordinary bone between it and the fossa for the hypophysis.

Paulli also mentions that the domestic cat, the Lion and the Tiger have each a small sinus in the hindmost part of the upper jaw. In the cat it forms a shallow pocket between the lateral plate of the ethmoid and the wall of the nasal cavity; in the Lion the sinus occupies the same position, and is high, but shallow. The Cheetah and Leopard have similar sinuses; in the former it is a small narrow cavity with the lachrymal and the orbital plate of the frontal for its outer wall, but not extending into the maxilla; in the latter it resembles that of the Lion, though it is probably somewhat lower in proportion. There are indications that this sinus is apt to vary with the individual, and not seldom it is difficult to find; indeed, it would appear to be absent in some specimens of Leopard and Lion, although it may never disappear entirely in the Cheetah.

The Lion agrees with the Leopard in its main features, but the sphenoidal sinus is larger. It excavates the root of the alisphenoid and may impinge slightly on the basisphenoid. In each of the specimens examined this sinus proved to be more extensive than that in the skull described by Paulli (*op. cit.*, p. 504). The posterior nares are higher than those of the Leopard, though not so high as those of the Cheetah.

III. BASICRANIAL AND OTIC REGIONS.

The basicranial and otic regions of the Cheetah differ in detail from those of the Lion and the Leopard. Many of the differences in the basi-cranium are due to the bending down of the face on the cranial axis, and, consequently, there is a shortening of the distances between the post-glenoid process and the bulla, and between the bulla and the occipital condyles. On the other hand, the relation of the anterior condyloid foramen to the foramen lacerum posterius is the same in the Leopard and the Cheetah, the former foramen opening into the latter.

The bulla is described (van Kampen, 1905; van der Klaauw, 1931) as being attached to the skull by the hinder leg of the tympanic alone, although Pocock (1916) mentions an anterior attachment to the basisphenoid. Doubtless the posterior tympanic attachment is the primary one in all three species, but the anterior leg of the tympanic is flattened and expanded at its tip to form a plate which is very closely applied to the postero-ventral surface of the root of the zygomatic arch, and which begins to enter into bony union with the squamosal whilst the animal is still sub-adult (*cf.* Lioness regd. 31.1.3.2. B.M. Zool. Dept.). In fully adult animals

vestiges of the joint remain as a fine crack, or suture, but a saw-cut is the only means of separating the two bones. The anterior attachment of the bulla to the basisphenoid is a sutural union, but the suture gradually becomes more and more indistinct until, in some old males, it disappears (Leopard, regd. 31.1.2.7 ; Cheetah, regd. 31.1.3.3, suture only just visible ; Lion, regd. 27.2.1.1., suture only just visible). Eventually, too, the lateral and posterior walls of the bulla fuse with the mastoid and paroccipital processes of the Leopard and Lion ; I have not observed this last attachment in the Cheetah. Hence it would seem to be more accurate to say that the primary attachment of the bulla to the skull is by means of the posterior leg of the tympanic, and that secondary attachments arise in the order, anterior leg of the tympanic, basisphenoid, mastoid, paroccipital process.

The greatest height of the bullae of the Lion and Leopard is about the centre, but in the Cheetah it is at about the anterior third of the length ; in addition the bulla of the Cheetah tends to be more compressed laterally than it is in the other two species. In all three species the degree of inflation is such that the bulla covers the foramen lacerum anterius (f. l. medius of many authors) and overhangs the foramen lacerum posterius.

The paroccipital processes are somewhat broadened, flattened, and applied to the posterior end of the bulla, but whereas in the Lion and Leopard, at least in old males, they may enter into bony union with the bulla, such union appears never to take place in the Cheetah. Moreover, the tip of the process is usually free in the Cheetah, whereas in the Lion and Leopard it is free only in old males. In all three species this process contains much cancellous tissue. The mastoid process is relatively small and closely applied to the bulla, though the tip is always free. The interior contains many large air-cells at its base about the level of the epitympanic recess. The cells diminish in size as they are traced towards the tip of the process, but the internal tissue always remains cancellous, more especially in the Cheetah.

Both the Leopard and the Cheetah display a pronounced groove for the tympanohyal, but whereas in the latter the groove remains widely open, with little or no tendency for its margins to turn in towards each other and so to form a tube, in the former the margins do turn inwards and come fairly close together, although they do not meet. Conditions similar to those in the Leopard obtain in a good many Lions, but in old males at least the formation of the tube is complete. The tympanohyal is cartilaginous throughout life according to Pocock (1916), but van Kampen (*op. cit.*, p. 508) and van der Klaauw (*op. cit.*, p. 242) say that it usually fuses with the bulla, and the latter suggests (p. 239) that Pocock is referring to the tympanostyloid cartilage. For my part, I have not been able to detect a satisfactory tympanohyal in any specimen examined. At the bottom of the vagina processus hyoidei there is occasionally a fissure which leads into the bulla medial to the posterior tip of the tympanic. This is a vestige of the fissura tympano-mastoidea through which Reichert's cartilage entered the middle ear of the embryo (*cf.* Lioness, 31.1.3.2. ; Leopardess, 36.2.8.20.). The pit for the hyoid is in advance of the stylomastoid foramen in the Lion and Leopard, but is medial, or slightly postero-medial to it in the Cheetah.

At the antero-medial margin of the bulla is a long process directed forwards and slightly inwards. This process, p. entotympanicus, is closely applied to the ventral surface of the basisphenoid by a dentate suture ; later in life the two bones fuse. Lateral to it, and at the anterior end of the furrow separating the ento- and ectotympanic bones, is another process, the processus styliformis (van Kampen, *op. cit.*, p. 501), to which the tensor veli muscle is attached ; it is small and often ill-defined in the Leopard, larger and laterally compressed in the Lion, and reaches its greatest development in the Cheetah in which it forms a stout dorso-ventral plate.

The bony tube (tuba ossea auditiva *sive* eustachii) is formed by the bulla and alisphenoid in all three species ; the petrosal plays no essential part in its construction, although it occasionally forms part of the roof of the extreme posterior portion when the alisphenoid is deficient.

The middle ear of the Felidae has often been described, but certain details still remain to be mentioned. The epitympanic recess is fairly deep in all three species; its lateral wall is normally formed by the squamosal, but occasionally the petrosal extends outwards and downwards to take a very small part in the formation of the wall. The chief difference between the Leopard on the one hand, and the Lion and the Cheetah on the other, is that whereas in the Leopard the roof of the fossa for the m. tensor tympani is much higher than that of the fossa for the head of the malleus, the other two species have both fossae of approximately the same height.

In Leopard and Cheetah the septum bullae is closely applied to the ventral surface of the petrosum and its free margin turns outwards. At the posterior end the margins of the mesial wall of the bulla and the septum are widely separated; as they pass forwards, they approximate so that a triangular slit is formed which is closed by the promontory of the petrosal, and the only direct communication between the two chambers of the bulla is at the posterior end. In the Lion, on the other hand, the septum does not meet the petrosal and the two chambers communicate freely along the whole length of the septum by a fissure which may be as much as 4 or 5 mm. wide at its widest part, and in no specimen examined is less than 2 mm. least width.

Hyrtl (1845) says that the fenestra cochleae, which is immediately in front of the opening by which the two chambers of the bulla communicate varies in its direction according to the species. He says that in the Lion the opening between the chambers is of a fair size and that the fenestra partly faces into the medial chamber, whereas in the Leopard the fenestra opens almost entirely into the medial chamber. van Kampen (*op. cit.*, p. 504) criticizes certain aspects of Hyrtl's results, which, he suggests, are to be explained by the difficulty of delimiting the two chambers of the bulla at the point where they communicate. A very simple method of estimating the position of the fenestra cochleae is to look through the external auditory meatus of the dried skull. Viewed in this manner, the f. cochleae and f. vestibuli are always visible, the former in part and the latter entirely, in both the Leopard and the Cheetah. As a general rule neither opening is visible in the Lion, although the f. vestibuli is to be seen with some difficulty. There appear to be two reasons for this. First is the purely mechanical one that the meatus is relatively narrower in the Lion and the rugged nature of the surrounding structures makes it difficult to examine the inside of the ear from an oblique angle; second, which may be verified by removing the medial wall of the bulla, is that the f. cochleae may be directed more to the inner chamber in the Lion than it is in the other two species. All three species have a variable number of crests and osteophytes springing from the walls of the medial chamber of the bulla; they are best developed in the Lion.

The petrosal bone of the Lion differs from that of the Leopard and Cheetah in a rich development of air-cells in its upper portion, whereas in the other two species such cells are few or absent.

IV. THE SKULL (INTERIOR) AS A WHOLE.

The details of the interior of the skull in sagittal section are shown in the plates accompanying this paper. The specimens there figured were photographed so that the skulls on Pl. 6 are all of the same basal length, and the endocranial casts on Pl. 7 are of the same overall length measured from the back of the cerebellum to the front of the olfactory bulb. Two features are immediately noticeable, namely, the different extent to which the face is bent down on the basicranial axis (least in the Leopard, greatest in the Cheetah), and the relative volume of the interior of the brain-case (least in the Lion, greatest in the Cheetah). The former is further illustrated in Fig. 2. Here the anterior and posterior ends of the basicranium have been arranged on the same horizontal, and the outlines drawn to the same basal length; the proportional lengths of the cranial bones are shown, as well as the relative heights of the posterior nares, and the brain-case, and it is evident that the skull of the Lion is more primitive than that of the Leopard, despite the greater degree of specialization involved in the bending-down of the face.

The primitive nature of the Lion is again noticed when the inside of the brain-case and the endocranial cast are examined. Not only is the relative volume of the brain smaller, but its anatomy is more primitive. For example, the cerebellum does not extend backwards along the medulla as much as it does in the Leopard and Cheetah, and, relative to the middle lobe, the anterior and temporal lobes are smaller and less inflated. Another primitive feature of the endocranial cast of the Lion is the length of the olfactory bulb as measured from the supraorbital sulcus.

The external features of the brain of the Cheetah are affected by the bending down of the face on the basi-cranial axis. This has prevented any real shortening of the olfactory lobe and has carried it downwards, so that the lobe itself is relatively as long as that of the Lion, although it is not so deep from above downwards, and is

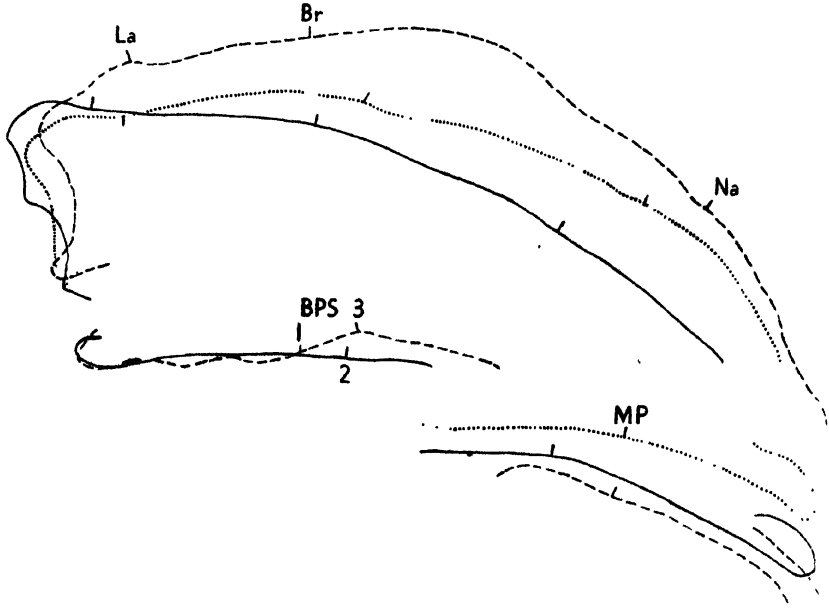

FIG. 2.—Superimposed outlines of median longitudinal sections of the skulls of Lion (full line), Leopard (dotted line), and Cheetah (broken line) drawn to the same basal length and with the anterior and posterior ends of the basicrania on the same horizontal. BPS indicates the suture between the basi- and pre-sphenoid bones (1 = Lion ; 2 = Leopard ; 3 = Cheetah). *La*, Lambda ; *Br*, Bregma ; *Na*, Nasion ; *MP*, Maxillo-palatine suture.

less in volume. Hence there is evidence to support the suggestion that the sense of smell is not so strongly developed in the Cheetah as it is in the Lion and Leopard. Another effect of the bending of the skull is to prevent the forward growth of the cerebrum, consequently the inferior surface of the anterior lobe, which is convex in the Lion, becomes concave as the brain moulds itself to the posterior wall of the orbit. A similar phenomenon is displayed by the Leopard, but in that species the flattening of the anterior lobe is entirely due to the forward growth of the cerebrum until it impinges on the orbital region.

The cerebral gyri and sulci are typical of the cats in general, but as the figures on Pl. 7 indicate, they are not always clearly reproduced on the endocranial cast, although with patience they can usually be made out (*cf.* Merriam & Stock, 1932, figs. 11, 135).

The angles between the various planes of the skull in median section are :—

	Lion	Leopard	Cheetah	Cat
Basicranium–Foramen magnum	93°	103°	94°	110°
Basicranium–Cribrif. plate	140°	134°	150°	155°
Basicranium–Facial axis	220°	153°	235°	145°
Basicranium–Tentorium (summit) ..	33°	40°	40°	—

The measurements are made according to Mivart (1881, p. 84, fig. 48), from whom the values for the domestic cat are taken. Reasonably to interpret these values is a matter of some difficulty because of the different specializations in each animal; at the same time, there are certain features to which attention may profitably be drawn. The angle of the foramen magnum is practically the same in the Lion and the Cheetah; in both of them it is about 10° less than in the Leopard, whereas the angle of the cribriform plate is greater in the same two species. The latter angle is clearly affected by the degree of bending down of the face on the basicranial axis, but the former seems to have different explanations in each of the three species. In the Lion the upright position of the plane of the foramen magnum is a primitive feature, whereas in the Leopard it has been pushed over backwards by the expansion in volume of the brain, especially the cerebellum. This expansion is at least as great. if not greater, in the Cheetah, yet the plane of the foramen magnum maintains the upright position which is regarded as primitive in the Lion. A possible explanation, already discussed by Haltenorth (1937, p. 217), is that the head and neck are held differently in this species, and it is very likely that this change in position prevented the expansion of the cerebellum having the same effect as it had in the Leopard. Similarly, the bending down of the face limited the possibility of forward expansion of the cerebrum. Nevertheless, the brain had to expand in one direction or another; it took the only path left open to it and expanded upwards, for the solidity of the basicranium prevented any expansion downwards. Hence the more nearly globular shape of the brain of the Cheetah compared with the shape of the brains of the Lion and Leopard.

The photographs on Pl. 6 illustrate another point of interest, namely, the relatively small size of the Lion's teeth. The second premolar is little more than a vestige in all the felines, but the third and fourth between them perform the whole work required of the cheek-teeth in these animals. The following figures are taken from the specimens shown on the plate, and the numbers in italics are the ratios when the basal length is taken as 100.

	Lion	Leopard	Cheetah
Basal length	305	183	164
	100	*100*	*100*
Greatest length of P 3–4	60	43	38·1
	19·7	*23·5*	*23·2*
Canine height.....	45·2	35	27·8
	14·8	*19·1*	*17*

These ratios do not support Haltenorth's contention that the teeth of the Cheetah are weak, for, if they are not so strong as those of the Leopard, they are certainly stronger than those of the Lion. Similar measurements taken from other skulls suggest that the upper limits of the ratios in the Lion are approximately equal to the lower limits in the Cheetah. Concerning the canines, there is the additional complication to be borne in mind, that the oldest and largest animals have often lost several millimetres of the tip of the tooth through wear.

V. DISCUSSION.

Of the three species here considered, the Leopard has the most 'normal' type of skull; the development of the brain, the angle between the basi-cranial and facial axes, the development of the sinuses, and the general structure of the skull are all those of an average feline. But the other two species show considerable deviation

from this type, the Lion being much more primitive and the Cheetah much more specialized. So far as the Cheetah is concerned, the specialization has long been marked by systematists by means of a distinct generic name, *Acinonyx*, but opinion generally is against according similar distinction to the Lion. Pocock, Haltenorth, and, most recently, Simpson, all include Lion and Leopard in the one genus *Panthera*. On the other hand, Haltenorth has clearly shown that the Lion is by far the most primitive of the great cats, and that conclusion is reinforced by the additional features here described. Indeed, the Lion is in its cranial characters farther removed from the Leopard than is the Cheetah from the Ounce (*cf.* Haltenorth, 1937): it differs from the Tiger as much as the Tiger differs from the Leopard, and more than the Puma differs from the Ounce. If Haltenorth is correct in this, and there is no evidence to the contrary, it seems out of scale to place the Ounce in the distinct genus *Uncia*, the Puma in *Puma* as a subgenus of *Panthera*, and yet to retain the Lion in *Panthera* s.s. along with the Tiger and the Leopard. In view of its isolation from the other species included in *Panthera* there is good reason for placing the Lion in the distinct subgenus *Leo* Oken, 1816, and if Simpson's cautious remark that the Jaguar 'perhaps merits subgeneric rank' be acted on, then it might be necessary to give the Lion the dignity of a distinct genus.

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EXPLANATION OF THE PLATES.

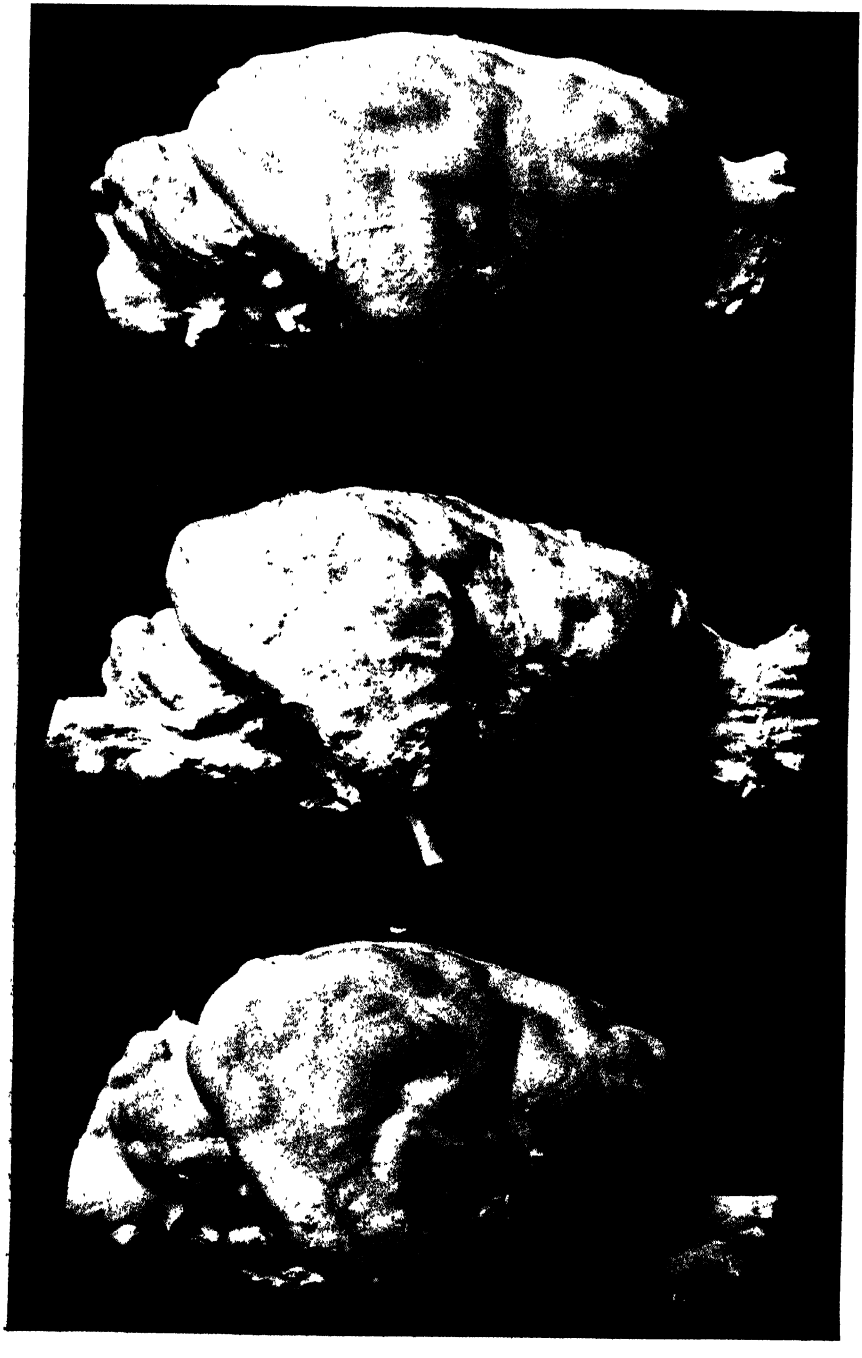
Plate 6.

Median longitudinal sections of the skull of Leopard (above), Lion (centre), and Cheetah (below) photographed to the same basal length. The relative sizes of the endocranial cavity, as well as the sinus in the nasal bone of the Cheetah, are clearly shown.

Plate 7.

Endocranial casts of Leopard (above), Lion (centre), and Cheetah (below) photographed to the same overall length measured from the back of the cerebellum to the front of the olfactory bulb.

SKULLS OF LEOPARD, LION AND CHEETAH.



ENDOCRANIAL CASTS OF LEOPARD, LION AND CHEETAH.

Further Notes on the Structure of the Bony Fishes of the Order Lyomeri (*Eurypharynx*).

By V. V. Tchernavin. (From the Department of Zoology, British Museum, Natural History.)

(Plate 8 and 8 Text-figures.)

(Read 8 May 1947.)

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1. Introduction.

My previous work on Lyomeri (Tchernavin, 1947) was handicapped by the scarcity of material, and so several obscure points in the structure of these extraordinary fishes could not be studied.

Through the kindness of Dr. Å. V. Tåning of the Marine Biological Laboratory in Charlottenlund Slot, I received several specimens of *Eurypharynx*, and Dr. Tåning gave me his kind permission to dissect some of them. An account of the results obtained from the dissection of the branchial region of *Eurypharynx* is given here.

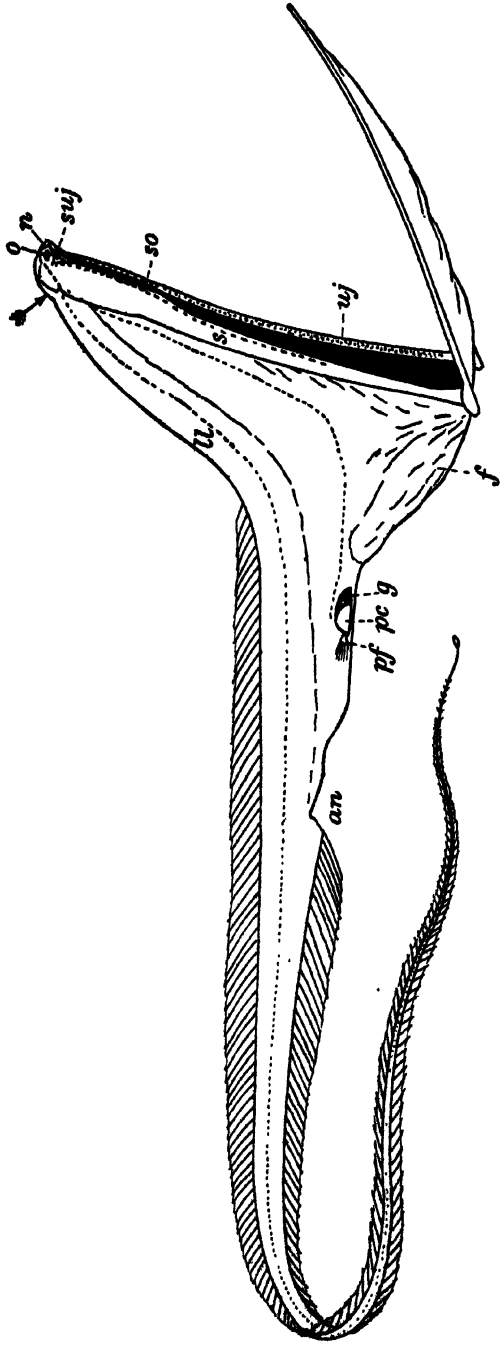
This present investigation deals mainly with the nature of the extra visceral cleft of *Eurypharynx* ; the relations of the facial nerve and the nerves of the vagus group to the visceral clefts ; and the vascular system of the branchial apparatus. I had in hand for this study specimens of the genus *Eurypharynx* only, and used mainly the specimens which were damaged during their capture or which had already been dissected by my predecessor in the study of the 'Dana' collection of Lyomeri. I dissected the specimens under a binocular microscope, but did not prepare sections, and I could not inject the blood vessels owing to the smallness of these vessels and the unsuitable condition of the material.

It is probable that using such a primitive method, I have missed some of the features of these fishes, or made some errors. I hope, however, that my description and figures of the structures concerned, of the course of the cephalic nerves, and of the main blood vessels are correct on the whole.

The work was done in post-war conditions, and with post-war equipment, of which the less said the better.

The figures are drawn by the writer. The photographs were taken by the official photographers of the British Museum (Natural History).

Acknowledgments.—I thank most warmly Dr. Å. V. Tåning for his kind permission to use for this investigation the material of *Eurypharynx* collected by the 'Dana' Expedition, and Prof. L. Bertin for sending me this material from Paris. I am much indebted to Dr. E. Trewavas for her kind interest in my work, help and advice.



TEXT-FIG. 1.—Diagrammatic drawing showing the general shape of *Eurypharynx*. Side view, slightly from the front. Mouth slightly open, and therefore the anterior part of the body is raised. Note that the upper jaw lies mesially to the suspensorium mandibulae and to the mandible. The posterior end of the cranium is shown by an arrow. Note that a large part of the body (containing about 20 vertebrae) separates the cranium from the branchial apparatus. *an*, anus; *f*, folds in the wall of the oral cavity; *g*, gills; *ll*, lateral line of the body; *n*., nostril; *o*, eye; *pc*. pericardium seen through the thin wall of the body; *pf*, pectoral fin; *s*., suspensorium mandibulae; *so*., infraorbital branch of the lateral line running along the bone acting as the upper jaw; *suj*, symphysis of the upper jaw; *vj*, upper jaw.

2. Nature of the extra (sixth) Visceral Cleft in *Eurypharynx*.

First of all it must be stressed here that all the numerous specimens of *Eurypharynx* of different sizes, collected in different regions, invariably have *six* branchial clefts and *five* holobranchs (Pl. 8, figs. A, B). All the six clefts and all the five holobranchs are functional, and none of them can be described as vestigial ; this is also confirmed by study of the branchial arteries.*

Two different ways of interpreting the extra cleft of *Eurypharynx* seemed to me possible (Tchernavin, 1947 p. 312).

(1) All six clefts of *Eurypharynx* are branchial clefts. If so, the ventral hyoid elements are completely missing, *the foremost branchial cleft is situated between the mandible and the first branchial arch*, and an extra, sixth, branchial cleft, and an extra posterior hemibranch, homologous to those found in some Selachians, are found in *Eurypharynx*, though never in all known recent and fossil Osteichthyes.

(2) The cartilages supporting the septum behind the foremost cleft are the ventral elements of the hyoid arch, and this cleft corresponds to the ventral part of the prehyoid cleft. If so, the five posterior clefts of *Eurypharynx* correspond to the usual branchial clefts of Osteichthyes ; and *Eurypharynx*, having the ventral part of the prehyoid cleft open, recalls to some extent the Acanthodians as described by Watson (1937) †.

Having no specimens for dissection during my previous study, I left this question open.

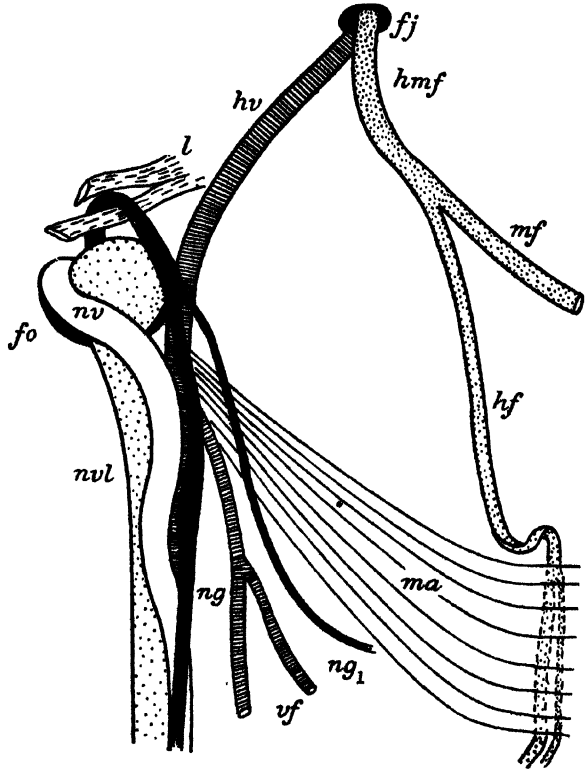
Relations of the facial nerve and of the nerves of the vagus group to the branchial arches.—The *truncus hyomandibularis* vii (*hmf.*) emerges through the jugular foramen (text-fig. 2, *fj*) ventrally to the head vein. After a short run it turns slightly outwards, soon dividing into two branches. One branch (*ramus mandibularis, mf.*), runs outwards close to the hind edge of the hyomandibular, enters from the inner side into this bone and passes out from the outer side of it, running towards its distal end. It gives off a branch which runs first further in the same direction along the suspensorium, and after passing the hyomandibulo-quadrate articulation, turns caudad along the inner side of the thin wall of the oral cavity. It gives branches to the series of the lateral line organs disposed between the suspensorium and the first branchial arch. The nerve runs dorsally to the foremost branchial cleft and passes beyond this cleft. It is probably the *ramus opercularis superfacialis* vii. The *ramus mandibularis facialis* runs further towards the distal end of the suspensorium and divides into two branches, which are probably the *rr. mandibularis internus* and *externus*. Apparently only one of them (*r. mandibularis internus*) reaches the lower jaw. At the distal end of the quadrate, this nerve runs along the posterior edge of this bone, then passes to its inner side, medially to the mandibulo-quadrate articulation and to the ligament attaching the palatine to the inner surface of the quadrate ; further the nerve runs along the inner side of the mandible.

The hyoid branch of the facial nerve (*r. hyoideus, hf.*) separates from the *truncus hyomandibularis* before the manidular nerve enters the hyomandibular bone, and runs caudad behind the hyomandibular. The hyoid nerve soon divides into two uneven branches. Both turn sharply dorsad and pass between the strong ligaments of the *m. adductor hyomandibularis* (*ma.*). Then they turn medially, towards the lateral dorsal aorta, and come close to it in the region of the first vertebra. They run further towards the tail dorsally to this artery. The smaller branch gives off a small twig (not seen on text-fig. 2) before reaching the *m. adductor hyomandibularis*, this twig subdivides and enters this muscle.

* Nussbaum-Hilarowicz (1923, p. 64, pl. ix, fig. 13) describes five branchial clefts in *Eurypharynx*, but on the figure, representing the *same specimen*, shows *six* branchial clefts. Rauther (1937, footnote on p. 243) doubts whether it is true that *Eurypharynx* has five holobranchs ; Regan (1912, pp. 347–49) and Berg (1940, p. 439) do not mention the sixth cleft of *Eurypharynx* in their descriptions of this group.

† The presence of a complete prehyoid cleft in Acanthodians is most emphatically denied by Prof. N. Holmgren (1942, pp. 144, 145).

The main trunk of the hyoid nerve runs further backwards, but already in the region of the ninth vertebra it becomes of smaller volume ; running further caudad it gives off a large branch which runs obliquely ventrad and caudad ; still further caudad, it divides into two branches which take a course in the same direction as the first branch. Thus, the hyoid nerve divides into branches running between the oblique transverse muscles of the wall of the gut, *in front of the foremost visceral cleft*, and does not pass beyond this cleft. This indicates that the oblique muscles, in front of the foremost visceral cleft, correspond to the hyoid muscles, that the ventral elements of the hyoid arch are missing, and that the foremost visceral cleft of *Eurypharynx* is the first branchial cleft.



TEXT-FIG. 2.—Diagram showing the position of the hyomandibular trunk (*VII*), the glossopharyngeal and vagus nerves and the head vein of the left side on the ventral surface of the cranium of *Eurypharynx*. ×10. *fj.*, foramen jugularis (in the prootic) ; *fo.*, foramen for the IX and X nerves (in the lateral occipital) ; *hf.*, hyoid nerve (*VII*) ; *mf.*, mandibular nerve (*VII*) ; *hmf.*, hyomandibular trunk (*VII*) ; *hv.*, head vein ; *l*, ligaments of the lateral muscle of the body ; *ma.*, *m. adductor hyomandibularis* ; *ng.*, glossopharyngeal nerve ; ng_1., branch of the glossopharyngeal nerve ; *nv.*, branchial trunk of the vagus nerve ; *nvl.*, lateral trunk of the vagus nerve ; *vf.*, *v. fascialis maxillaris*.

The glossopharyngeal nerve (text-figs. 2, 3, *ng.*) leaves the skull through the same foramen (*fo.*) in the lateral occipital as the vagus nerve (Tchernavin, 1947, p. 315). It emerges anteriorly to the ganglion of the latter nerve, then turns ventrad between the two ligaments (*l.*), of the dorso-lateral muscle of the body, close to the place where these ligaments are attached to the cranium. It turns then sharply caudad, passing ventrally to the head vein but dorsally to the lateral aorta, and lying between

these two vessels. It soon gives off a branch (ng_1.) which runs outwards. The main trunk of the nerve has a ganglion-like swelling and runs further straight caudad, ventrally to the head vein and dorsally to the lateral aorta, in close vicinity to these vessels.

Reaching the junction of the lateral dorsal aorta with the first epibranchial artery, the ninth nerve turns ventrad following closely the course of the artery, gives off a pre-trematic branch which runs towards the anterior end of the foremost branchial cleft, while the post-trematic nerve passes into the gill septum between the first and second branchial clefts. The nerve passes mesially to the efferent dorsal loop *d*, but laterally to the main efferent branchial artery. After passing through the branchial septum it turns at about a right angle forwards, and runs towards the head close to the ventral branch of the first branchial efferent artery (*ha.*).

The vagus nerve (text-figs. 2, 3, *nv.*, *nvl.*) passes out through a foramen (*fo.*) on the lateral occipital (the foramen is common with the ninth nerve). A large ganglion is found just outside this foramen. It is apparently an expansion of the *ramus lateralis vagi* (*nvl.*). The main lateral branch of vagus (*nvl.*) runs straight caudad medially and dorsally to the cardinal vein along the vertebral column. It gives off at regular intervals branches running obliquely backwards and dorsad straight to the lateral line organs. The foremost pair of these nerves arises opposite the first vertebra. The branchial trunk of the vagus (*nv.*), after leaving the cranium, turns round to the ventral side of the ganglion and passes straight caudad, dorsally to the ninth nerve.

Before reaching the region of the branchial clefts a nerve (nv_1., *truncus branchialis primus*) separates from the dorsal side of the main trunk of the nerve, passes downwards laterally to this nerve, to the cardinal vein, and to the lateral aorta, and follows very closely the first epibranchial artery. It divides then into three branches, the anterior (pre-trematic) reaches the first branchial arch; the post-trematic branch runs into the septum between the second and the third branchial clefts, passes through the septum and turns towards the cranium, its course resembling closely that of the post-trematic branch of the glossopharyngeal nerve. A third branch of the *truncus branchialis primus* separates from it and runs backwards into the third branchial arch. The *truncus branchialis secundus* (nv_2.) separates from the dorsal side of the trunk of the vagus nerve somewhat further caudad and runs into the third branchial septum. The branchial trunk of the vagus nerve continues its course towards the tail; reaching the level of the sixth branchial cleft it gives off a bunch of four nerves which run ventrad. The anterior of these nerves (nv_3.) passes into the fourth branchial arch and gives off a twig, which runs into the septum between the fifth and sixth branchial clefts. The next nerve (nv_4.) passes into the fifth branchial arch. The two posterior nerves (nv_5. and nv_6.) pass behind the sixth cleft. The main trunk of the vagus much diminished in volume follows its caudad course close to the coeliaco-mesenteric artery (*cma.*).

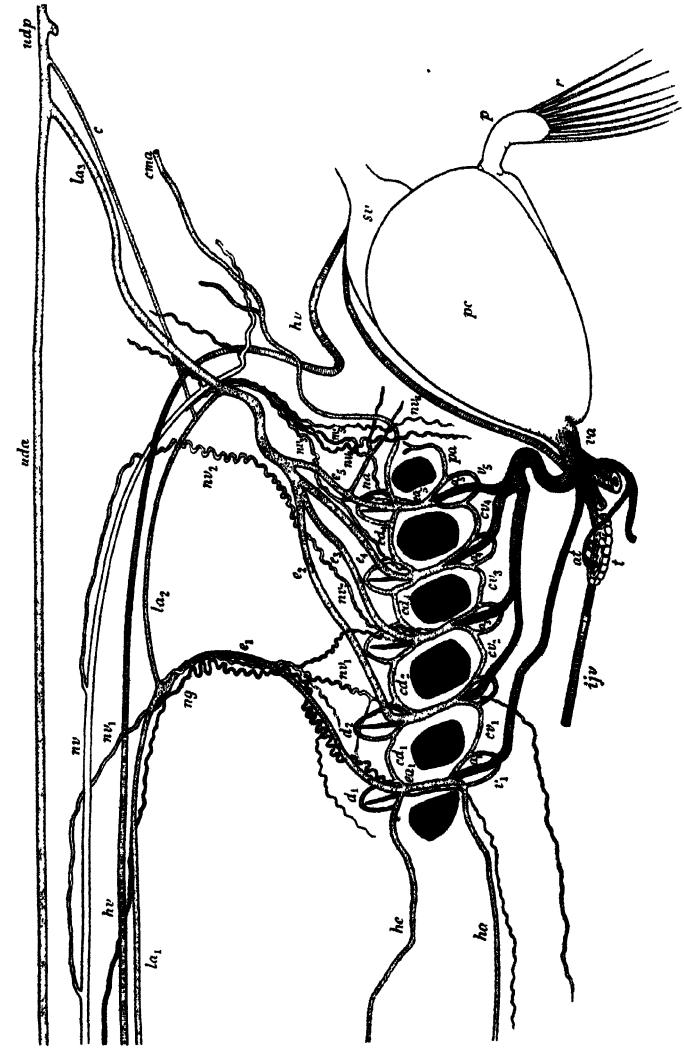
Thus, the course of the facial, glossopharyngeal and vagus nerves show that the foremost branchial cleft of *Eurypharynx* corresponds to the first branchial cleft, and that the sixth cleft is an additional branchial cleft which is never found in Osteichthyes.

3. Gills.

I described in an earlier paper (Tchernavin, 1947, p. 302) the position and the general structure of the branchial chambers in Lyomeri. From better material in hand I add here a brief description of the gills of *Eurypharynx*.

Eurypharynx has five well-developed holobranchs situated behind the five anterior branchial clefts; there is no gill behind the sixth cleft. All five holobranchs have the same structure.

The branchial arches are much reduced in *Eurypharynx* and not ossified. They are represented by separate cartilaginous rods extending along the branchial septa, close to the inner surface of the latter. The mucous membrane covering the inner



TEXT-FIG. 3.—Vascular system and the nerves of the branchial region of *Eurypharynx*; right side; seen from within; diagrammatic, simplified; (afferent and efferent vessels of the gill filaments, and the arteries issuing from the unpaired dorsal aorta to the segments of the body not shown). About × 6.

Afferent vessels dotted dark, efferent dotted lighter, veins striated, glossopharyngeal nerve black, vagus nerve white. Branchial clefts black.

a_1-a_5, afferent branchial arteries; *at*, artery of the thyroid gland; **c.**, commissural vessel uniting the lateral dorsal aorta with the unpaired dorsal aorta; cd_1–cd_4, lateral commissural vessels (dorsal series) of the efferent arteries; *cma.*, coeliaco-mesenteric artery; cv_1–cv_4, lateral commissural vessels (ventral series) of the efferent arteries; d_1–d_5, dorsal arches of the efferent arteries; e_1–e_5, epibranchial arteries; ea_1–ea_5, efferent branchial arteries; *ha.*, ventral branch of the first branchial artery; *he.*, dorsal branch of the first branchial artery; *hv.*, head vein (jugular, cardinal); *ijv.*, inferior jugular vein; la_1–la_5, parts of the lateral (paired) dorsal aorta; *na.*, branch of the 5th epibranchial artery (nutritive artery of the heart ?); *ng.*, glossopharyngeal nerve; *nv.*, branchial trunk of the vagus nerve; nv_1–nv_5, branches of the vagus nerve; *p.*, base of the pectoral fin; *pa.*, posterior ventral artery passing below the sixth gill cleft; *pc.*, pericardium; *r.*, rays of the pectoral fin; *sv.*, sinus venosus; v_1–v_5, ventral arches of the efferent arteries; *va.*, ventral aorta; *uda.*, anterior part of the unpaired dorsal aorta; *udp.*, posterior part of the unpaired dorsal aorta.

surface of the septa is thick and much folded, while the cartilages forming the arches are soft and transparent, more slender than a branchial artery. When the cartilage is isolated from the surrounding tissues, it twists and bends. It is thus rather difficult to trace the branchial skeleton without preparing sections. As far as can be seen from a dissection, the branchial skeleton of an arch consists on each side of a single cartilage, which is about as long as the septum ; it is of irregular thickness, and two narrow isthmuses can be distinguished, subdividing the cartilage into three parts. It may be, however, that these subdivisions are due to the shrinking of the soft cartilage in spirit.

The cartilages of the branchial arches are quite separate from each other, from the cranium and from the vertebral column. There are no ventral branchial elements, and the right and left semi-arches are thus also quite separate. I found such cartilaginous rods behind the first, second, third, fourth, and fifth branchial clefts ; I have not found any cartilages behind the sixth cleft. But it is not impossible that I could have missed them.

Nussbaum-Hilarowicz (1923, p. 66) describes four branchial arches in *Eurypharynx*; Bertin (1936, p. 23) writes that *Eurypharynx* has five branchial arches.

The gills of *Eurypharynx* are not attached to the skeleton of the branchial arches, and the gill-rays supporting the gill filaments are broadly separated from the cartilage of the branchial arch (Nussbaum-Hilarowicz, 1923, p. 66). The gill is not confined to the septum between two clefts but extends along the wall of the gut dorsally and ventrally beyond the septum. I counted the gill-filaments in the posterior hemibranch of the third cleft ; seven filaments are attached to the wall of the gut above the septum, ten are attached to the septum itself, and nine to the wall of the gut below the septum. Thus, the additional parts of the gill below and above the septum play as important a rôle in the breathing process as the part of the gill on the septum itself.

The gills of *Eurypharynx* consist of filaments which have substantially the same structure as in other Osteichthyes ; it seems that there is no need to use a special nomenclature for their description (comp. Nussbaum-Hilarowicz, 1923, pp. 64–66 ; Bertin, 1934, p. 23). The filaments are long and the gill rays supporting these filaments are soft. Thus the filaments are not rigid and not projecting into the branchial cavity at a right angle to the branchial arch ; they bend freely and hang downwards forming a kind of neatly arranged, wavy branch or tuft. The filaments of the additional parts of the gill are attached to the wall of the gut in a different way from those attached to the septum itself ; but the alternate arrangement of the filaments of the two hemibranchs of one gill is very distinct throughout the gill, so that it is quite clear to which holobranch each single filament belongs (compare Bertin, 1934, p. 34). The basal parts of the filaments of the two hemibranchs in the part of the gill attached to the septum, overlap each other in the usual teleostean way, for the afferent and the efferent arteries pass along the middle of the branchial septum (text-fig. 4), and the afferent and efferent vessels of the filaments issue from this midline. The gill-filaments of the additional parts of the gill have a different disposition. Their afferent arteries run along the midline of the gill (between the two hemibranchs,) but their efferent vessels originate from an arch-like efferent vessel (text-fig. 4, d_2., v_2.). Therefore the bases of the filaments of the two hemibranchs are arranged in such a way that their afferent ends are disposed along the midline of the gill, but their efferent ends are set apart along the arches of the efferent artery.

The branchial lamellæ are well developed, but appear thicker than usual in Osteichthyes (this is also found in some other deep sea fishes). Nussbaum-Hilarowicz (1923, p. 67) described their minute structure.

I did not study the muscular system of *Eurypharynx*, and mention here only some of the uncommon features of their branchial muscles which I saw when I examined the branchial arteries. The branchial muscles are not attached to the skeleton of the arches. Each branchial cleft is surrounded by two muscles overlapping each other in a way similar to the *mm. sphincter branchialis anterior* and

profundus of *Petromyzon*. A large muscle extends (dorso-ventrally) along the branchial septum, recalling by its position the *m. constrictor interbranchialis* of *Petromyzon*. Two longitudinal muscles run above and below the branchial clefts. All these muscles are controlled by the IXth and Xth nerves. There is a series of transverse muscular fibrils in the wall of the pharynx in front of the foremost branchial cleft; they are innervated by a branch of the VIIth nerve.

The muscle arising from the hind edge of the sixth branchial cleft is described with the heart.

4. Vascular System * (text-figs. 3, 4, 5, 6).

Afferent arteries.—The ventral aorta (*va.*) after leaving the heart almost at once divides dorso-ventrally into three trunks.

(*a*) The most ventral one is of small diameter; it issues from the left side of the ventral surface of the ventral aorta. After a short run downwards and forwards as a single vessel, it divides into two arteries. The left vessel enters the left longitudinal ventral muscle of the body in front of the heart, the right (*at.*) passes along the right side of the thyroid gland (*t.*) and divides completely into small branches entering into the gland. This vessel has no further extension.

The origin of the common trunk of these vessels varies in specimens; in one specimen it issues from the ventral side of the left first afferent artery, in another specimen from the common root of the four posterior afferent arteries (2nd–5th branchial arteries). However, it originates always from the ventral side and very close to the heart, its further course is always the most ventral one, and its branches have always the same relation to the ventral muscles and the thyroid.

(*b*) The pair of vessels carrying the blood to the foremost holobranchs issue from a short common trunk. After a long run forwards under the branchial region, these vessels turn upwards at almost a right angle, towards the foremost gills, forming the first pair of afferent arteries ($a_{1.}$).

(*c*) The most dorsal division of the ventral aorta is also very short, and subdivides into a pair of large vessels. At their origin these vessels are twisted in such a way that the one originating from the left side passes to the right half of the branchial apparatus, and that originating from the right side to the left half. The further course of these vessels can be seen on text-figs. 3, 5 B. Each vessel subdivides into two smaller vessels; the anterior one gives off the second and the third afferent branchial arteries and the posterior one the fourth and the fifth afferent branchial arteries.

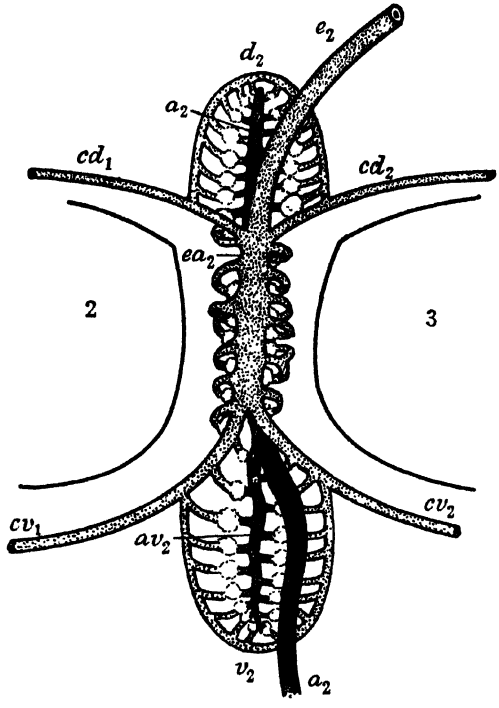
The afferent arteries themselves have some peculiarities which must be described (text-fig. 4). They have all five the same structure. The artery passes mesially to the ventral arch (*v.*) of the afferent artery, then it enters the gill septum and runs upwards laterally to the efferent artery; it extends upwards beyond the septum between the limbs of the dorsal arch (*d*) of the efferent artery. Before entering into the gill septum, the afferent artery gives a short branch (*av.*) which turns sharply downwards, and runs parallel to the afferent artery, but in an opposite direction, inside the ventral efferent arch (*d.*). This branch cannot be seen in text-fig. 3 (inside view of the branchials), being hidden behind the main trunk of the artery, but it is shown in text-figs. 4 and 6.

The thyroid gland in *Eurypharynx* (*t.*) is apparently supplied with blood directly by an afferent artery and thus can be described here. The gland is situated just in front of the heart on the ventral side of the body, close to the left side of the inferior jugular vein (*ijv.*) and dorsally to it. The gland together with the adjoining vessels, is enveloped in a rather loose sheath of connective tissue. To the naked eye the gland appears as a compact organ, light orange in colour. It is longer than broad, its length exceeds the greatest length of a branchial cleft. Under a microscope it can be seen that the gland consists of rounded follicles arranged in three

* A brief account of the vascular system of *Eurypharynx* was published in 'Nature' (Tchernavin, 1946).

irregular longitudinal rows. The follicles are loosely connected with each other. The right afferent artery of the most ventral arterial trunk (*at.*) passes close along the side of the gland and divides into small twigs which sub-divide again, entering into the gland. The artery has no further extension.

Nussbaum-Hilarowicz (1923, p. 68, pl. ix, fig. 12) studied the morphology and the minute structure of this gland in *Eurypharynx*. He found that the thyroid is situated in " un épaississement spécial du tissue conjunctif de la paroi d'un diverticulum pharyngein " and that the gland is connected anatomically with the respiratory organs.



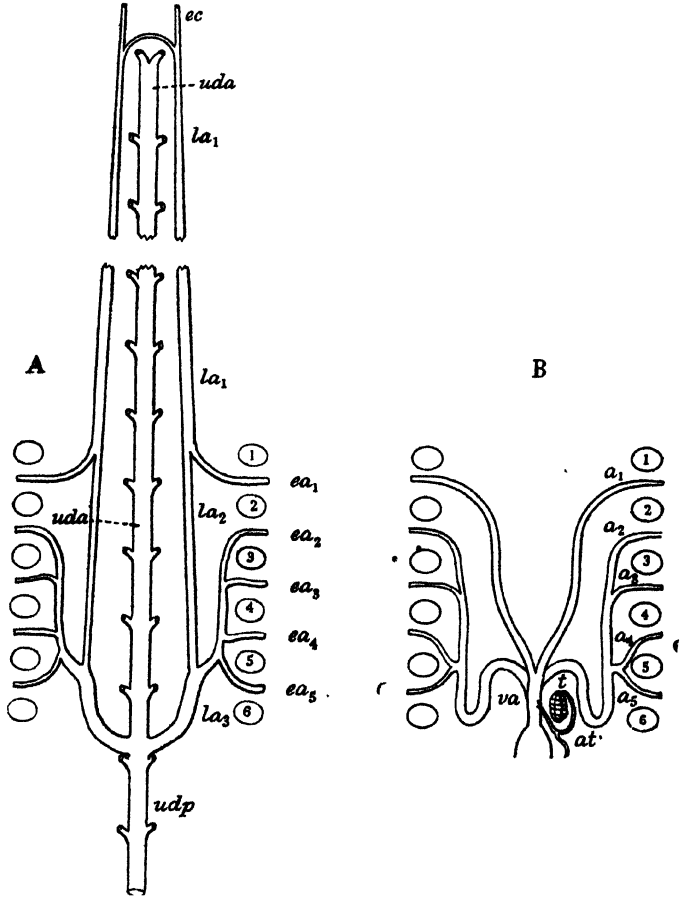
TEXT-FIG. 4.—Arteries of the second branchial arch of *Eurypharynx*. Inside view ; right side. Diagrammatic. × 15. Lettering as in text-figure 3 and in key, p. 392.

The fact that the thyroid retains its connection with the gut, suggests a primitive state of this gland in *Eurypharynx*. Nussbaum saw large blood vessels connected with the gland, but does not mention what these vessels are ; as already mentioned, they are branches of an afferent artery (*at.*).

Efferent arteries.—The main vessels of the five efferent arteries run in the septa behind the 1st–5th branchial clefts mesially to the afferent arteries. I could not make certain whether these vessels are single or consist of two vessels united together. Dorsally the efferent arteries are continuous with the epibranchial arteries, but give off each a pair (right and left) of lateral commissural vessels, running above the branchial clefts. Ventrally each efferent artery divides into two lateral commissural vessels running below the branchial clefts. Thus the efferent arteries of each cleft unite above and below the branchial clefts, forming a series of vascular loops round the 2nd–5th branchial clefts. These loops are very similar to those found in Selachians. The foremost efferent artery sends two vessels towards the head, one

(*he.*) passing above and the other (*ha.*) below the foremost cleft. The fifth afferent artery sends two vessels running towards the tail, above (*cma.*) and below (*pa.*) the 6th branchial cleft.

Beside the five vascular loops round the branchial clefts, two series of five dorsal, and of five ventral smaller loops are found above (*d.*) and below (*v.*) the branchial septa. These loops are formed by arch-like vessels uniting the lateral commissural branches of the efferent arteries. They are connected with the additional parts of the gills situated above and below the gill-septa.



TEXT-FIG. 5 (A, B).—Diagram of the efferent (A) and the afferent (B) arterial systems of *Eurypharynx*, simplified, not to scale; A, dorsal view; B, ventral view. For lettering see text-figure 3, or the key to the figures on p. 392.

The dorsal branch of the first efferent artery (*he.*) passes above the 1st branchial cleft and runs along the wall of the oral cavity towards the cranium. After passing about twice the distance between this cleft and the cranium it gives off a small branch running upwards, and close to it a second markedly larger one. The first branch soon divides in the wall of the oral cavity into smaller vessels, the second branch runs first ventrad at almost a right angle to the main vessel, then turns caudad and divides into small twigs in the pharyngeal wall not quite reaching the

branchial apparatus. The main vessel of the artery follows its almost straight course forwards, gives off another small branch running dorsally, and reaches the suspensorium mandibulae as a very small vessel. I could not follow its further course.

The ventral branch of the first efferent artery (*ha.*) passes below the foremost branchial cleft and runs in the pharyngeal wall obliquely forwards and downwards towards the lower jaw. At the end of its long course, close to the mandibulo-quadrate articulation, it divides into small branches in the ventral wall of the oral cavity close to the inferior jugular vein.

I could find nothing suggesting that these arteries or their branches supply with blood any remnants of a gill.

The dorsal posterior branch of the fifth branchial artery (*cma*) passes above the sixth branchial cleft and then runs obliquely upwards and backwards. It is soon joined by a branch of the vagus nerve which runs close to it. The artery turns then caudad. It corresponds probably to the coeliaco-mesenteric artery. I did not follow its further course.

The ventral posterior branch of the fifth branchial artery (*pa.*) has a short run. It passes below the sixth branchial cleft and then turns sharply upwards behind the sixth branchial cleft, where it divides into two small branches.

Epibranchial arteries.—The first epibranchial artery (e_1) reaches the lateral aorta independently from other epibranchial arteries. The second and the third epibranchial arteries meet together in a short common trunk which is soon joined by the fourth and fifth arteries. This trunk runs upwards and backwards, unites with the rather thin middle part of the lateral dorsal aorta (la_2) and follows its course as the hind part of the lateral aorta towards the midline of the back where it reaches the unpaired dorsal aorta, and closes the *circulus cephalicus* posteriorly.

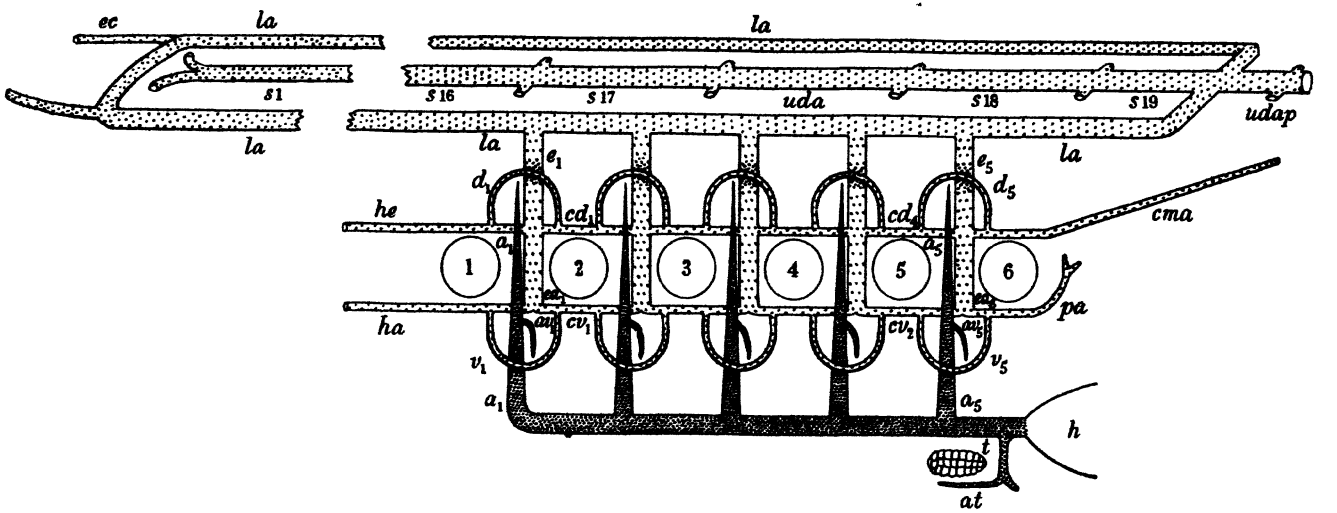
Lateral dorsal aortae.—Three distinct parts can be distinguished in the main trunk of the lateral (paired) dorsal aorta ; a large vessel (la_1) which extends from the dorsal end of the first epibranchial aorta to the base of the cranium ; a narrower vessel (la_2) which extends between the dorsal end of the first epibranchial artery to the common trunk of the four posterior arteries ; and a large vessel (la_3) which is continuous with the latter trunk and runs dorsad to the median, unpaired dorsal aorta. Reaching the base of the cranium, the lateral aorta gives off a vessel (*ec.*), the orbital artery (external carotid), which runs forwards under the cranium and enters the orbit. The lateral aorta turns mesially, gives off another branch and enters the cranium where it probably meets its fellow from the other side, closing the *circulus cephalicus* anteriorly. I had no opportunity of seeing the actual union of the lateral aortae in the cranium and did not follow their further course inside the cranium.

The median (subvertebral, or unpaired) dorsal aorta has two parts (text-figs. 3, 5 A, 6). The anterior part (*uda.*) extends from the cranial base backwards between the limbs of the lateral aorta to the posterior end of the *circulus cephalicus*. The posterior part of the unpaired aorta (*udp.*) extends from the posterior end of the *circulus cephalicus* to the end of the tail. The unpaired dorsal aorta divides anteriorly into two branches, and gives off a pair of lateral branches to each metamere. Nineteen or twenty pairs of such vessels are found in its anterior part (*uda.*) running between the lateral dorsal aortae.

The median dorsal aorta has no direct communication with the first epibranchial artery, and is mainly supplied with blood from the four posterior branchial arteries.

The median dorsal aorta has from its right side a thin commissural vessel (*c.*) which unites it with the narrow portion of the lateral dorsal aorta.

In a carefully dissected specimen it can be seen that this vessel (text-fig. 3, *c.*) unites with the median dorsal aorta between the dorsal ends of the two lateral dorsal aortae. (In this specimen the mouth of the right lateral dorsal aorta lies slightly in front of the left one ; text-fig. 3.)



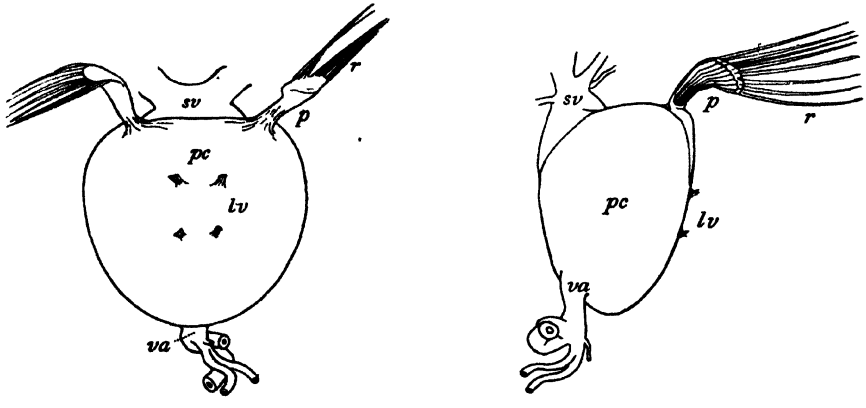
EXT-FIG. 6.—Diagram of the arterial system of the branchial region of *Eurypharynx* simplified, not to scale, no division of the ventral aorta and no unions of the epibranchial arteries before they reach the lateral aorta are shown. Left side slightly from above. For lettering see text-figure 3 or the key to the figures on p. 392.

ec, external carotid,

A vessel (text-fig. 3, *na.*), the homology of which is not clear to me, and which I could not follow along its whole course, originates from the fifth epibranchial artery and runs backwards and downwards towards the heart. It soon divides into two branches which run nearly parallel to each other. They both come close to the dorsal side of the pericardium, but I could not see their further course. It seems possible that they are the nutrient arteries of the heart.

The veins of the head.—The head vein (anterior cardinal or the superior jugular) leaves the cranium through the jugular foramen, mesially to the articulation of the hyomandibular with the cranium, and at about the vertical level of the articulating groove for the condyle of the hyomandibular. This groove is unusually deep, its roof lies dorsally to the jugular foramen, while its ventral edges lie ventrally to this foramen. In this respect the position of the jugular foramen in relation to the horizontal level of the articulating groove of the hyomandibular differs from that typically found in Osteichthyes (comp. de Beer, 1937, pp. 410, 411). However, this unusual relation may be due to the great flatness of the cranium of *Eurypharynx*, while the condyle of the hyomandibular is very large and the groove receiving it very deep. The facial nerve passes through the jugular foramen ventrally to the head vein.

The inferior jugular vein is single posteriorly in the region of the branchial apparatus and of the heart, but paired anteriorly.



TEXT-FIGS. 7, 8.—Diagrams showing the relation of the pectoral fins to the pericardium of *Eurypharynx*. × 3·3. 7, ventral view ; 8, lateral view (right side).
lv., ligaments of the ventral muscle of the body ; *p*, base of the pectoral fin ; *pc.*, pericardium ; *sv.*, sinus venosus ; *va*, ventral aorta.

5. RELATION OF THE PECTORAL FINS TO THE PERICARDIUM.

The heart in *Eurypharynx* lies far away from the cranium on the vertical of about the 18th vertebra, very close to the ventral surface of the body. The pericardium is clearly visible through the thin transparent ventral wall of the body. The main protection of the heart from the outside is the very thick wall of the pericardium.

The close relation of the pericardium to the pectoral fins is unusual. The pectoral fins are small, and their basal parts are lobate. The fin rays are simple and not segmented. Though small, the fins are functional and each ray has its muscles well developed (apparently, two attractors, and a dilatator). The basal lobe of the fin extends obliquely inwards, passes through the peritoneal septum and inserts into the ventral wall of the pericardium close to its posterior end.

The elastic fibrillae of the pericardial wall extend right into the basal parts of the fins, and unite it firmly with the pericardium. The connection of the basal lobe of the pectoral fin with the pericardium is very firm ; some of the elastic fibrillae of the pericardial wall pass along the sides of the lobe, some cross the lobe.

The pair of ventral muscles passing along the midline of the ventral side of the body are long and narrow. These muscles are firmly attached to the ventral side of the pericardium (each muscle by two ligaments, text-figs. 7, 8, *lv*). The contraction of these muscles would affect the heart by pressing on it ventrally and lifting it upwards. Another narrow long muscle issues from the ventral edge of the sixth gill cleft, passes close but laterally to the posterior wall of the pericardium and to the base of the pectoral fin, then turns round the ventral side of the pericardium, where it spreads out fan-like and is inserted into the ventral longitudinal muscle of the body. By the contraction of this muscle the posterior part of the heart and the pectoral fins would be pulled upwards into the branchial chamber. As far as I am aware, in this relation of the pectoral fins and of the ventral muscles of the body to the pericardium, *Eurypharynx* is unique among fishes.

6. Summary and Conclusions.

As I mentioned in my earlier paper (Tchernavin, 1947), the Lyomeri disagree with many characteristics of the class Osteichthyes, to which they can be referred as having true bones with cells, the head vein passing out of the cranium medially to the articulation of the hyomandibular with the otic region of the cranium, and having the nostrils on the dorsal side of the head.

In Lyomeri the mandibular arch has no direct contact with the cranium. The dorsal end of the quadrate unites intimately and directly with the ventral end of the hyomandibular (no symplectic) ; the dorsal ends of the palatine bones (apparently fused with the suborbitals) meet each other under the cranium and are attached by a ligament to the ventral side of the cranium. There is no secondary upper jaw (premaxillary and maxillary). The infraorbital lateral line runs along the front part of the upper jaw. The bones of the lower jaw have no connection with the lateral line system. The hyoid arch consists of one element only—the hyomandibular. It is situated well in front of and far above the branchial cavity, and has no contact with the latter. There is no hyoid operculum (no operculum, sub- or interoperculum, no branchiostegals) ; the preoperculum is also missing. The branchial apparatus of Lyomeri differs most substantially from that of Osteichthyes. The branchial clefts are situated far behind the cranium and close to the ventral midline of the body, the branchial arches having no contact with the cranium nor with the vertebrae. As the ventral hyoid elements are missing, and the hyomandibular is situated well above the level of the branchial arches, the foremost branchial cleft lies between the mandible and the first branchial arch. *Eurypharynx* has *six* functional branchial clefts and *five* holobranchs. The hyoid branch of the facial nerve does not extend behind the foremost visceral cleft. The glossopharyngeal nerve runs into the septum dividing this cleft from the second one ; branches of the vagus nerve run behind the third, fourth, fifth, and sixth clefts. Thus, this foremost cleft is a branchial cleft, homologous to the first branchial cleft of other fishes, and the sixth branchial cleft of *Eurypharynx* is homologous to the sixth branchial cleft of some Selachians ; no such cleft is found in Osteichthyes.

The branchial arches are not ossified ; they have no elements uniting them ventrally, and the right and left parts of the arches are completely separated from each other. Each such semiarch consists of a single thin rod extending along the branchial septum (*Eurypharynx*). There is apparently no arch behind the sixth branchial cleft. The branchial arches are not <-shaped. The septa between the branchial clefts are broad and fleshy. The branchial muscles are not attached to the branchial arches ; they surround the branchial clefts, forming a kind of sphincter round each cleft. Two longer muscular bands pass above and below the clefts.

The gills extend dorsally and ventrally beyond the branchial septa on the wall of the gut. There is a special arrangement of the afferent and efferent vessels for supplying these additional parts of the gills.

The vascular system is unusual. The single ventral aorta is very short, and almost at once after leaving the heart divides vertically into three short afferent

trunks. The shortest of the ventral aortae recalls that of Dipnoi. The most ventral afferent artery supplies the thyroid gland with blood. There are five pairs of afferent branchial arteries, the foremost of which runs behind the first branchial cleft. Such an arrangement is never found in Osteichthyes. The afferent branchial arteries extend dorsally beyond the branchial septum and supply with blood the dorsal additional parts of the gills. Each afferent artery before entering the gill septum gives off a branch running in the opposite direction (ventrad) and supplying with blood the ventral additional part of the gill.

The efferent system presents a singular combination of features which, individually, are characteristic of Selachians, Osteichthyes and Cyclostomata, and of features which are unique among fish-like animals.

The efferent branchial arteries, five in number, are united by longitudinal commissural vessels above and below the gill-clefts, forming loops round the clefts, recalling those of Elasmobranchs. Above and below the branchial septa, arch-like vessels unite the commissural efferent vessels, forming thus a dorsal and ventral series of five additional loops, which collect the blood from the additional dorsal and ventral parts of the gills. As far as I know, no such additional series of loops are found in other fishes.

As in other Osteichthyes there is a paired lateral dorsal aorta, which forms the *circulus cephalicus*, emitting no lateral vessels to the muscular segments; it is supplied with blood mainly from the first epibranchial artery. Beside the paired lateral aorta, an unpaired dorsal aorta extends from the posterior end of the *circulus cephalicus* to the base of the cranium, between the limbs of the lateral dorsal aorta. This anterior part of the unpaired dorsal aorta gives off nineteen or twenty pairs of intersegmental arteries to the metameres of the body. Posteriorly the dorsal aorta extends as in other fishes. The unpaired dorsal aorta is supplied with blood, mainly from the common trunk of the four posterior epibranchial arteries. No such arrangement is found in Osteichthyes. But a similar structure is found in Myxine, and rudiments of the anterior part of the unpaired dorsal aorta are found in some Selachians, and Selachian embryos (Dorn, 1885, fig. 3; Ayres, 1879, pp. 197, 220; Holmgren, 1946, pp. 65–67). Among Osteichthyes only a minute rudiment, possibly of this vessel, is found in the common eel (*Anguilla*) (Ridewood, 1899, p. 949, pl. lxiv, fig. 16).

It seems worth mentioning that the epibranchial vessels of *Eurypharynx* present an almost mirror image of the trunks of the afferent arteries. The first branchial afferent and efferent arteries are separated from the four others. The four posterior afferent arteries have a common trunk, which subdivides into two twigs, from which the second and the third, and the fourth and the fifth arteries issue. The efferent arteries of the second and third arches unite into a common vessel, which then receives the fourth and the fifth efferent arteries, forming a common trunk for these four vessels.

The jugular vein passes out of the cranium through the jugular foramen with the hyomandibular nerve medially to the articulation of the hyomandibular with the cranium (as in other Osteichthyes). The inferior jugular (cardinal) vein is unpaired posteriorly (in the region of the branchial apparatus) but paired in front.

The lobate basal parts of the pectoral fins unite with the outer side of the pericardial wall in *Eurypharynx*. In *Saccopharynx* (Tchernavin, 1947) the basal parts of the pectorals articulate *laterally* (not mesially) with a reduced piece of the pectoral girdle, which apparently corresponds to the scapula. I found no secondary shoulder girdle in Lyomeri.

In my earlier paper I have shown also that in Lyomeri the bones of the cranium articulate movably with each other, so that the cranium can markedly change its shape; Lyomeri have no supraoccipital, no ossified lateral ethmoids, and the parasphenoid is very small with no lateral processes (*Eurypahrynx*), or absent (*Saccopharynx*); finally, the cover bones on the dorsal side of the cranium are unusual and their homologies are not clear. One has to remember also that the fin rays of

Lyomeri are ossified but not segmented and not branched, in disagreement with one of the main charateristics of Osteichthyes.

Where can the Lyomeri be placed in the system of Fishes ? It seems that there is no ground for relating the Lyomeri to any of the known orders of Osteichthyes, and that the Lyomeri can be readily opposed to all known Bony Fishes. If the Lyomeri are included in the group Osteichthyes on the ground of their ossified skeletons (which is not a sufficient character), and owing to the mesial position of the head vein in relation to the hyomandibular (which is an important feature), the main characteristics of the class Osteichthyes must be revised.

Such fundamental characters of Osteichthyes as the presence of a hyomandibular operculum, symplecticum, parasphenoid, secondary upper jaw, secondary shoulder girdle, lepidotrichian type of fin rays, no more than five branchial clefts and no more than four and a half gills, reduced and <-shaped branchial septa, efferent arteries separated from one another, and the absence of the median anterior unpaired aorta, can no longer be used as features characterizing the Osteichthyes, if the Lyomeri are included in this class.

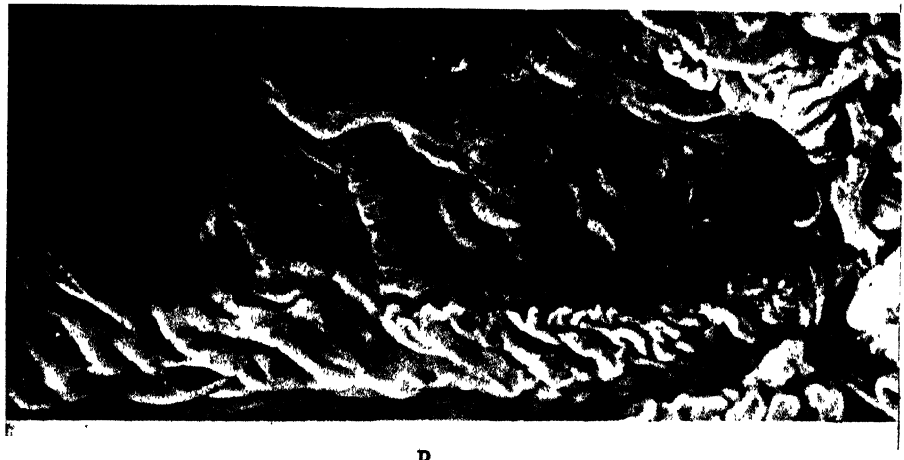
One can see also that by the Lyomeri having several Selachian characteristics, the differences between the Osteichthyes and Selachians are less definite.

A study of the development of Lyomeri would be of great help for a judgment on their relationship with other fishes. But all that is known about the development of Lyomeri is that their larva is " Leptocephalus "-like.

7. Key to the Figures.

a_1–a_5	first-fifth afferent branchial arteries.
an.	anus.
at.	artery of the thyroid gland.
av_1–av_5.	ventral branch of the afferent artery.
c.	commissural vessel uniting the lateral dorsal aorta with the unpaired dorsal aorta.
cd_1–cd_4.	lateral commissural dorsal vessels of the efferent arteries.
cma.	coeliaco-mesenteric artery.
cv_1–cv_4	lateral commissural ventral vessels of the efferent arteries.
d_1–d_5.	dorsal arches of the efferent arteries.
e_1–e_5.	epibranchial arteries.
ea_1–ea_5.	efferent branchial arteries.
ec.	orbital artery (external carotid).
f.	folds in the wall of the oral cavity.
fj.	foramen jugularis (in the prootic).
fo.	foramen for the IX and X nerves (in the lateral occipital).
g	gills.
ha.	ventral branch of the first branchial efferent artery.
he.	dorsal branch of the first branchial artery.
hf.	hyoid nerve (*VII*).
hv.	head vein (jugular, cardinal).
hmf.	hyomandibular trunk of the facial nerve.
ijv.	inferior jugular (cardinal) vein.
l.	ligaments of the lateral muscle of the body.
la_1, la_2, la_3.	parts of the lateral (paired) dorsal aorta.
ll.	lateral line.
lv.	ligaments of the ventral muscle of the body.
ma.	*m. adductor hyomandibularis*.
mf.	mandibular nerve (*VII*.)
n	nostril.
na.	branch of the 5th epibranchial artery.
ng	glossopharyngeal nerve.
ng_1	branch of the glossopharyngeal nerve.
nv.	branchial trunk of the vagus nerve.
nv_1–nv_5.	branches of the vagus nerve.
nvl.	lateral vagus nerve.
o.	eye.
p.	base of the pectoral fin.
pa.	posterior ventral artery passing round the sixth branchial cleft.
pc.	pericardium.
pf.	pectoral fin.
r.	rays of the pectoral fin.
s.	suspensorium mandibulae.
so.	infraorbital branch of the lateral line.
sv	sinus venosus.
suj.	symphysis of the upper jaw.
t.	thyroid gland.
v_1–v_5.	ventral arches of the efferent arteries.
va.	ventral aorta.
vf.	facial vein (?).
uda.	anterior part of the unpaired dorsal aorta.
udp.	posterior part of the unpaired dorsal aorta.
uj.	upper jaw.

A



B

A. THE GILLS OF *EURYPHARYNX*. B. THE GILL CLEFTS OF *EURYPHARYNX*.

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EXPLANATION OF THE PLATE.

Plate 8.

A. The gills of *Eurypharynx*; *in situ*; left side. The fold covering the gills removed. 8. In front of the first holobranch the foremost branchial cleft can be seen; behind the fifth holobranch the sixth cleft is seen. The lower (ventral) part of the fifth holobranch is partly covered by the gill filaments of the fourth holobranch.

B. The gill clefts of *Eurypharynx*, right side. 8. The gut is dissected and the inner apertures of the six branchial clefts are seen from the inside of the gut. Gill filaments are seen through the clefts.

Some Roundworms and Flatworms from the West Indies and Surinam. I. Nematodes and Acanthocephala.

By H. A. Baylis, M.A., D.Sc., Department of Zoology, British Museum (Natural History).

(With 12 Text-figures.)

[Read 8 May, 1947.]

This paper is the first of several in which it is intended to report on some helminths and free-living flatworms collected by Mr. Ivan T. Sanderson, mainly in Surinam (Dutch Guiana) in 1938, but partly also in the West Indies in 1937. The Cestodes will be dealt with in another paper by the present writer, and the Trematoda and Turbellaria in papers by Mr. S. Prudhoe.

The following is a classified list of the species of parasitic Nematodes and Acanthocephala included in the collection, with the hosts from which they were obtained. Unless otherwise stated, they were all collected in Surinam, at localities in the ' flood-plains ' within forty-five miles of Paramaribo.

The type-specimens of the new species described are in the British Museum (Natural History).

NEMATODA.

	Host.
Ascaridae.	
Toxocara mystax (Zed., 1800).	Felis pardalis.
Contracaecum sp., larva.	Tupinambis nigropunctatus.
Amplicaecum alatum, sp. n.	Tupinambis nigropunctatus.
Heterakidae.	
Ascaridia galli (Schrank, 1788).	' Wild turkey ', Mt. Aripo, Trinidad.
Aspidodera raillieti Travassos, 1913.	Marmosa cinerea, Didelphis marsupialis azarae.
Strongyluris sp. (♀♀)	Polyderus marmoratus, Diego Martin, Trinidad.
Spinicauda spinicauda Olfers, in Rud., 1819.	Tupinambis nigropunctatus.
Kathlaniidae.	
Cruzia tentaculata (Rud., 1819).	Marmosa cinerea, Didelphis marsupialis azarae.
Oxyuridae.	
Enterobius minutus (Schneider, 1866).	Alouatta macconnelli.
Ancylostomatidae.	
Ancylostoma braziliense Gomez de Faria, 1910.	Euprocyon cancrivorus.
Ancylostoma caninum Ercolani, 1859.	Euprocyon cancrivorus.
Diaphanocephalidae.	
Diaphanocephalus galeatus (Rud., 1819).	Tupinambis nigropunctatus.
Trichostrongylidae.	
Heligmodendrium aripense, sp. n.	Sciurus aestuans, Mt. Aripo, Trinidad.
Spiruridae.	
Protospirura muris (Gmel., 1790).	Rattus rattus, ' wild var. ' Mt. Commissar, Haiti.
Parabronema bonnei (van Thiel, 1925).	Alouatta macconnelli.
Physaloptera retusa Rud., 1819.	Tupinambis nigropunctatus.
Physaloptera mirandai Lent and Teixeira de Freitas, 1937.	Marmosa cinerea.
Physaloptera ? dilatata Rud., 1819 (1 ♂).	Cebus ? fatuellus.
Physaloptera ? muris-braziliensis Dies., 1861.	Sciurus aestuans, Mt. Aripo Trinidad.

Filariidae.	
Dipetalonema gracile (Rud., 1819).	Saimiri sciurea.
? Dipetalonema [? Molinema] sp. (♀♀).	Coendou prehensilis.
Skrjabinofilaria skrjabini Travassos, 1925.	Marmosa cinerea.
? Oswaldofilaria sp. (♀?).	Tupinambis nigropunctatus.
Philometridae.	
Micropleura vazi Travassos, 1933 (♀♀).	Caiman sclerops.
Trichinellidae.	
Trichuris ? minuta (Rud., 1819) (♀?).	Didelphis marsupialis azarae.
Trichuris ? gracilis (Rud., 1819) (♀?).	Dasyprocta agouti.

ACANTHOCEPHALA.

Oligacanthorhynchidae.	
Hamanniella microcephala (Rud., 1819).	Didelphis marsupialis azarae
Prosthenorchis elegans (Dies., 1851).	Saimiri sciurea.
	Mystax midas.

There follow descriptions of the two new species, and notes on a few of the other forms.

NEMATODA.

AMPLICAECUM ALATUM, sp. n. (Figs. 1–3).

Of this species seven males and four females were found in the stomach of *Tupinambis nigropunctatus* near Paramaribo, Surinam.

The males measure about 48–70 mm. in length, the females about 82–90 mm. The greatest thickness, which occurs in the posterior region of the body, is 0·6–0·97 mm. in the male and 0·8–1·17 mm. in the female. The transverse striations on the cuticle of the body are coarsest in the anterior region, where the intervals between them reach 7–10 μ. The anterior end is always curled dorsally, and is provided with well-developed lateral cervical alae. These begin at the base of the lips, and extend back for a distance considerably greater than the length of the oesophagus, gradually becoming narrower and finally disappearing. In a female in which they were measured their length was about 6·5 mm. Their greatest width is 0·1–0·12 mm. They are marked throughout with transverse striations, much closer together than those on the body.

There are well-developed interlabial grooves at the bases of the lips, bounded by prominent cuticular flanges. In a dorsal view (fig. 1) the interlabia are not very prominent, and are almost hidden by the angles of the dorsal lip. In lateral view, however, they are more conspicuous, and form the widest part of the head, which here measures 0·2–0·27 mm. across in the male, and 0·29–0·34 mm. in the female. The anterior border of each lip is deeply notched. The general shape of the dorsal lip (fig. 1) is roughly hexagonal. Its pulp is produced internally into two anterior processes. Externally it bears a pair of apparently simple papillae, while each ventro-lateral lip has a large subventral and a very small lateral papilla. The dentigerous ridges are well developed.

The oesophagus measures 2·7–4 mm. in length in the male and 3·6–4·4 mm. in the female. There is no ventriculus, but a conspicuous valve at the junction of the oesophagus with the intestine. From this point a wide intestinal caecum runs forward on the left side of the oesophagus for a distance of 1·6–2·5 mm. in the male and 2·3–3·15 mm. in the female. The nerve-ring is situated at 0·5–0·75 mm., the excretory pore at 0·6–0·98 mm., and a pair of cervical papillae at 0·9–1·25 mm. from the anterior extremity. These papillae appear to terminate on the dorsal surfaces of the alae, not far from the body-wall.

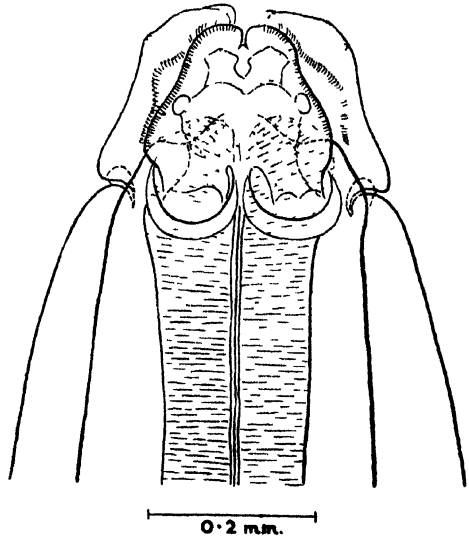


FIG. 1.—*Amplicaecum alatum*. Anterior end of female ; dorsal view.

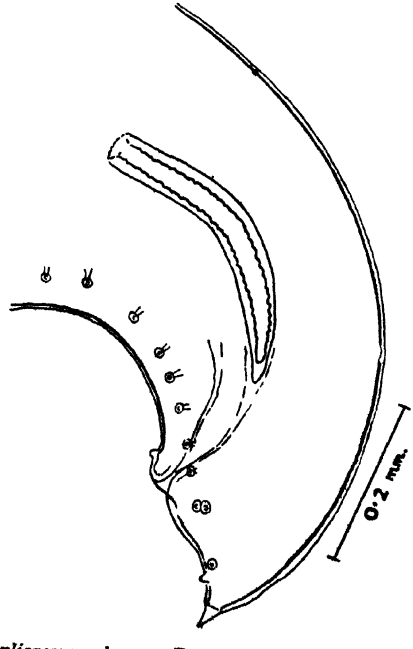


FIG. 2.—*Amplicaecum alaum*. Posterior end of male ; lateral view.

The tail, in both sexes, is very short and conical, with a terminal spike. In the male it measures 0·13–0·17 mm. in length. There are four pairs of small postanal papillae (figs. 2, 3), the two most anterior papillae on each side being almost at the angles of the cloacal aperture and placed so close together as almost to form a double papilla. On the anterior lip of the cloaca there is a median papilla, and at this level there begins a simple series of about 20–25 preanal papillae on each side, gradually becoming more widely spaced anteriorly. The spicules are equal and very short and stout, measuring (in a straight line from root to tip) about 0·24–0·35 mm. The coils of the genital tube occupy little more than the posterior third of the body.

The tail of the female is 0·2–0·29 mm. long. The vulva is situated at rather more than one-third of the total length from the posterior end of the body (at a distance of 33–38 mm. from the extremity), and is slightly prominent. The vagina has thick, muscular walls, and runs posteriorly from the vulva for about 1·5 mm. before passing into a long common uterine trunk. This runs back for about a further 11 mm. before giving off the two parallel uterine branches, which are about 12 mm. long and quite straight. At its posterior end each branch expands somewhat to form a club-shaped receptaculum seminis about 0·5–0·6 mm. wide, and then narrows suddenly into a muscular oviduct about 0·6–0·8 mm. long and 0·1–0·15 mm. wide. Each ovarian tube, where it joins this duct, is also expanded into a club-shaped swelling about 0·4–0·5 mm. wide. The ovarian tubes are long and much convoluted,

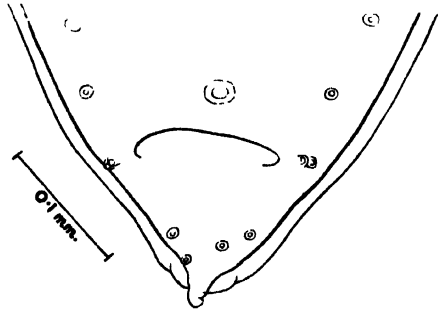


FIG. 3.—*Amplicaecum alatum*. Posterior end of male; ventral view.

their most anterior loops extending to about 2 mm. behind the vulva, and their most posterior loops (representing the narrow distal portions of the ovaries) to within about 0·7–1·5 mm. of the posterior extremity. The eggs are ovoid, with externally mammillated shells, and are of very uniform size, measuring about 0·07–0·076 × 0·05–0·052 mm. Their contents *in utero* are either unsegmented or in the first stages of segmentation.

The genus *Amplicaecum* Baylis, 1920, appears at present to contain eight species *, and to be unknown from the New World. With the exception of the genotype, *A. colurum* (Baylis, 1919) all the species are recorded from reptiles or amphibians. *A. colurum*, of which the male is unknown, occurred in an African eagle, and may possibly have been a pseudoparasite, the real host perhaps being a reptile or amphibian. The presence of broad cervical alae distinguishes *A. alatum* from all the known species except, possibly, *A. excavatum* (Hsü and Hoeppli, 1931). In this species such alae are not mentioned, but figures given by Hsü and Hoeppli (1931, Pl. V, figs. 20, 21) suggest that they may be present. The male of *A. excavatum*,

* '*Amplicaecum*' *ardei* Layman and Andronova, 1926, appears, from the figures, to be a species of *Contracaecum* in which the oesophageal appendix has not been observed. Possibly it is a synonym of *C. microcephalum* (Rud., 1809). For the synonymy of *A. involutum* (Gedoelst, 1916) see Baylis (1940), p. 404.

however, has no less than 55–58 pairs of preanal and six pairs of postanal papillae. The shortness of the spicules further distinguishes *A. alatum* from this species and from *A. varani* Baylis and Daubney, 1922, *A. involutum* (Gedoelst, 1916), *A. novem-papillatum* Sandground, 1933, and *A. schoutedeni* Baylis, 1940. There remain *A. brumpti* Khalil, 1926, and *A. cacopi* Chatterji, 1936, in both of which the male has only five pairs of preanal papillae and apparently lacks the median precloacal papilla.

ANCYLOSTOMA BRAZILIENSE Gomez de Faria, 1910, and A. CANINUM Ercolani, 1859.

These two species occurred in the small intestine of a Crab-eating Raccoon (*Euprocyon cancrivorus*) near Paramaribo, together with *Diphyllobothrium*. *A. braziliense* was present in greater numbers than *A. caninum*, of which only three specimens were found. One specimen of *A. braziliense* had attached itself to a *Diphyllobothrium*. The crab-eating raccoon is probably a new host for both of these species, though *A. caninum* has been recorded by Chitwood (1932) from *Procyon lotor* in captivity in North America.

HELIGMODENDRIUM ARIPENSE, sp. n. (Figs. 4–8.)

Of this species two males and seven females (with some fragments) were obtained from the large intestine of a squirrel (*Sciurus aestuans*) at Mt. Aripo, Trinidad. The collector's notes indicate that the worms were red during life.

The two males measure respectively 8·7 mm. and 10·3 mm. in length, and 0·15 mm. and 0·2 mm. in maximum thickness. The females measure 12·3–15·2 mm. in length. The greatest thickness in the female usually occurs near the posterior end (fig. 8), where there is a slight swelling just in front of the vulva, measuring about 0·2–0·25 mm. in diameter. There is a cephalic inflation of the cuticle (fig. 4), measuring 0·04–0·064 mm. in diameter and varying in length from about 0·046–0·062 mm. This variation is partly due to the fact that the mouth is sometimes retracted within the cephalic inflation.

The cuticle of the body bears, throughout almost the whole of its length, 18 longitudinal crests (fig. 5), 16 of which are low, while two are very prominent and fused in such a way as to form a great thickening (figs. 5 and 8, *s.*), with a wide V-shaped groove running along it, in a subventral position on the left side of the body. The transverse striations are particularly conspicuous in these crests, and appear as rod-like supporting structures within them. There are from 5 to 7 such 'rods' in a space of 20 μ, so that the striations may be said to be at intervals of about 2·9 to 4 μ. Sometimes, especially towards the anterior end of the body, the crests, or rather the series of 'rods', have an interrupted appearance, such as has been described in several species of the genus. This, however, is possibly an optical result of the crests being slightly wavy, so that parts of them are seen in profile and parts in optical section. At the posterior end of the body, in the female, the crests tend to run round the body in a sinistral spiral (fig. 8).

The oesophagus, which is slightly club-shaped, measures 0·47–0·49 mm. in length in the males and 0·5–0·55 mm. in the females. The nerve-ring is situated at about 0·26–0·3 mm. from the anterior extremity. Further back, at about 0·43–0·53 mm. from the extremity, there is a pair of extremely prominent cervical papillae (fig. 6), measuring up to 20 μ in length and usually bifurcate, the longer termination being posterior. The excretory pore is a little behind these papillae.

The bursa of the male and its rays (fig. 7) are slightly asymmetrical, being a little longer on the right side than on the left. The dorsal ray is relatively very large, and of the general form characteristic of the genus, with the externo-dorsal rays arising from its two main branches. Prebursal papillae were not seen. The spicules are relatively slender and measure 0·63 mm. in length. The 'telamon' could not be clearly made out in the two specimens available.

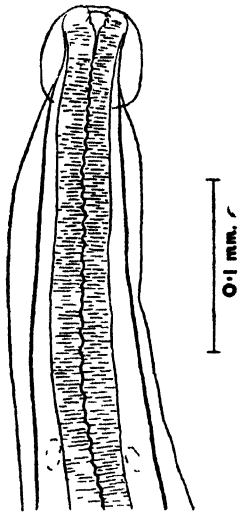


Fig. 4.

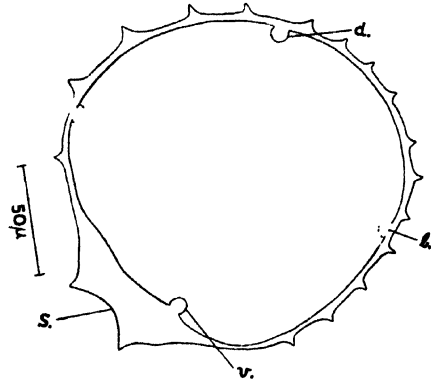
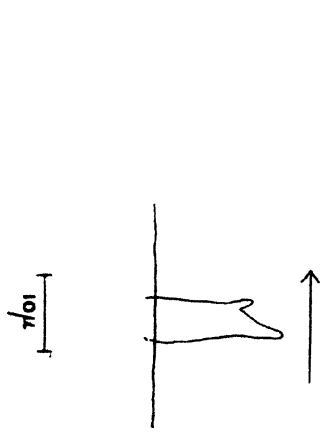


Fig. 5

FIG. 4.—*Heligmodendrium aripense.* Anterior end of female; dorsal view.
FIG. 5.—*Heligmodendrium aripense.* Transverse section of female, in middle region of body, showing the cuticle and longitudinal fields only. *d*, dorsal, *l*, lateral, and *v*, ventral fields; *s.*, subventral thickening of cuticle.



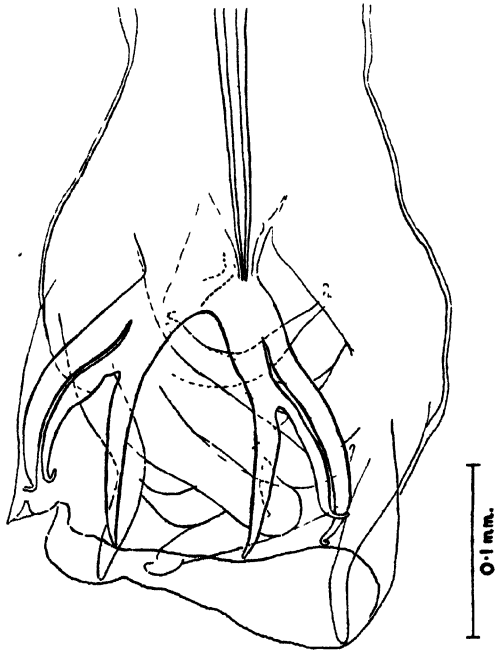


Fig. 6. Fig. 7.

FIG. 6.—*Heligmodendrium aripense*, female. Cervical papilla. The arrow points towards the anterior end.

The tail of the female is about 0·07 mm. long. The vulva is situated at 0·2–0·22 mm. from the posterior end, and has a prominent posterior lip. The ovejector has a length of about 0·4–0·45 mm. The thin-shelled eggs are oblong-oval and measure about 0·076–0·086 × 0·038–0·04 mm. Their contents are segmenting *in utero*.

The genus *Heligmodendrium* Travassos, 1937, originally contained two species, *H. elegans* (Trav., 1921) and *H. hassalli* (Price, 1928). Four others have since been added to it, viz. *H. interrogans*, *H. hepaticum* and *H. oliveirai* Lent and Teixeira de

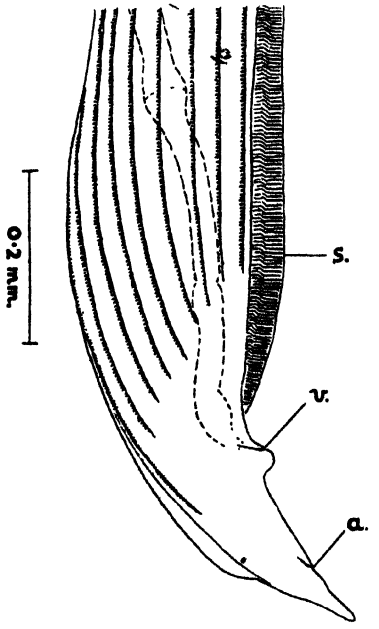


FIG. 8.—*Heligmodendrium aripense*. Posterior end of female; lateral view. *a.*, anus; *s.*, subventral thickening of cuticle; *v.*, vulva.

Freitas, 1938, and *H. crucifer* Travassos, 1943. Of these six species, *H. hepaticum* and *H. oliveirai* are recorded from *Sciurus aestuans* in Brazil (i.e. from the same host as the present material), while *H. hassalli* is recorded from *Sciurus carolinensis* in the United States. The present species is of larger size than any of those mentioned, though a fairly close approach to it is made by *H. hepaticum*. The most striking feature, however, which distinguishes the present form from all the others, is the length of the spicules in the male. In this respect the nearest known species appears to be *H. crucifer*, which, although the worm is only of about half the size, has spicules measuring up to 0·59 mm. in length *. In none of the other forms do the spicules attain a length of much over 0·4 mm.

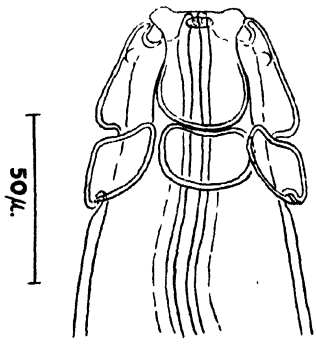
PARABRONEMA BONNEI (van Thiel, 1925). (Figs. 9–12.)

van Thiel (1925) described this species, under the name of *Squamanema bonnei*, from a Howler Monkey (*Alouatta* [*Mycetes*] *seniculus*) from Surinam. Yorke and Maplestone (1926) and Baylis and Daubney (1926) regarded the genus *Squamanema*

* Travassos gives '0·038–0·059' mm., but it is clear from his figure that there has been a displacement of the decimal point.

as a probable synonym of *Parabronema* Baylis, 1921, but hitherto no further description of it seems to have appeared. The present collection contains a number of specimens collected from the stomach of *Alouatta macconnelli* in Surinam by Mr. Sanderson, who describes them in his notes as ' bright red and clear ' when alive. Among the large number of females preserved, only two males have been found. Advantage has been taken of this material to make a careful re-examination of the species, and there seems to be no doubt that it is a *Parabronema*. It possesses all the characters regarded as typical of that genus, and its only striking peculiarity is the presence of a great thickening of the cuticle along one side (the right side) of the body, as described by van Thiel. This thickening, which doubtless represents an exaggerated lateral ala, is regarded as a feature of merely specific importance. The following description supplements, and in some respects corrects, that of van Thiel.

The two males measure respectively 10·1 and 11·8 mm. in length, and the females up to 30 mm. or more. The maximum thickness of the body, including the lateral cuticular thickening, is about 0·22 mm. in the male and up to, or slightly over, 0·3 mm. in the female. The transverse cuticular striations are at intervals (in the



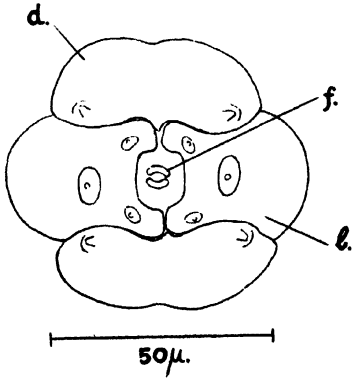


FIG. 9.—*Parabronema bonnei*. Anterior end of female; lateral view.
FIG. 10.—*Parabronema bonnei*. Anterior end of female; frontal view. *d.*, dorsal shield; *f.*, false lips; *l.*, lateral lip.

middle region of the body) of about 4 μ in the male and 6–7 μ in the female. The lateral cuticular thickening, or ' ala ', on the right side of the body has a maximum thickness of about 0·026 mm. in the male and up to 0·06 mm. in the female. The marked longitudinal incision in the thickening described and figured by van Thiel has not been observed in the present specimens (fig. 11).

van Thiel describes the mouth as triangular and surrounded by six lips. Actually (figs. 9, 10) there are paired lateral lips, and dorsal and ventral ' shields ', as described by the writer (1921) for the genotype of *Parabronema* (*P. indicum*). The ' shields ', however, in *P. bonnei*, scarcely overlap the lips. The arrangement of the cephalic papillae is exactly the same, each lateral lip bearing three papillae, and the dorsal and ventral shields two each. The auricular appendages of the head, in *P. bonnei*, are somewhat simpler in structure, their posterior edges not being folded or grooved. The distance from the anterior extremity to the posterior edges of these appendages is about 0·06–0·07 mm. in both sexes. The width of the head, at the level of their posterior edges, is about 0·064 mm. in the male and 0·08 mm. in the female. The mouth itself, i.e. the actual opening of the buccal cavity or ' pharynx ', is at the summit of a rather prominent papilla between the lips (fig. 9), and the cuticular lining of the pharynx appears to be produced

slightly further dorsally and ventrally than laterally, so as to form a pair of minute 'false lips' at right angles to the lips proper (fig. 10, *f.*). The pharynx is relatively long in this species, measuring about 0·18 mm. in length, as stated by van Thiel. The oesophagus (measured from the extremity of the head, and thus including the pharynx) is 1–1·4 mm. long. It consists of two portions, both muscular, the anterior portion being of about the same length as the pharynx and considerably narrower than the posterior portion. The anterior portion is surrounded by the nerve-ring at a distance of about 0·24 mm. from the extremity of the head. The excretory pore, which is very inconspicuous, is at about the same level, and the cervical papillae (also inconspicuous) slightly further back.

The tail of the male (fig. 12) measures 0·25–0·27 mm. in length, and there are well-developed and somewhat asymmetrical caudal alae. The whole ventral surface of the caudal region is covered with interrupted, longitudinal cuticular ridges. van Thiel states that the spicules are unequal and dissimilar, but does not give their lengths. In the two males in the present collection, the left spicule measures about 2·2 and 2·1 mm. respectively, and the right spicule about 0·37 and 0·31 mm. Both spicules are provided with alae. The left spicule measures about 8 μ in width, the

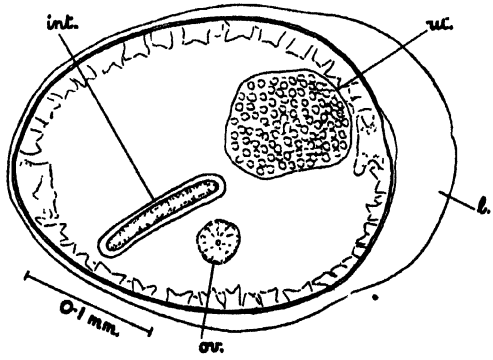


FIG. 11.—*Parabronema bonnei*. Transverse section of female, in middle region of body. *int.*, intestine; *l.*, lateral thickening of cuticle; *ov.*, ovary; *ut.*, uterus.

right about 18 μ. At its tip, however, the right spicule narrows suddenly and forms a small hook. There is a small, triangular accessory piece, not mentioned by van Thiel. This measures about 0·03 mm. in length. The arrangement of the caudal papillae of the two sides is much more asymmetrical in the present specimens than is indicated in van Thiel's figures. It is, however, quite typical for a *Parabronema*. In particular, the position of the first pair of postanal papillae, with their peduncles lying transversely across the ventral surface and their terminations almost in the middle line, the right papilla a considerable distance behind the left, is highly characteristic. van Thiel does not seem to have observed the large median preanal papilla, which appears to have paired terminations, as in the genotype. The number of papillae is otherwise as described by van Thiel—four pairs of lateral and preanal or adanal papillae, two pairs of large postanal and a group (apparently two pairs) of minute papillae near the extremity of the tail. The sucker-like 'muscles' described by van Thiel in the posterior pair of large postanal papillae have not been observed.

The tail of the female measures about 0·21–0·25 mm. in length. It is always curved towards the dorsal side, and has a bluntly-rounded tip and apparently a pair of minute subterminal papillae. van Thiel's description of the vulva as being situated at the posterior third of the body is quite erroneous. The vulva is very

inconspicuous, but is situated at 2–3·3 mm. from the anterior extremity (i.e. not far behind the junction of the oesophagus and intestine). The vagina is narrow and muscular, and runs almost straight back for a distance of at least 2·2 mm., with a U-shaped bend in its course at 0·8–1 mm. from the vulva. The arrangement of the genital tubes has not been made out in detail, owing to the opacity of the specimens. The thin-walled uterine branches are crammed from end to end with short, cylindrical, blunt-ended embryos measuring about $40\,\mu \times 8\,\mu$ and apparently not enclosed in membranes.

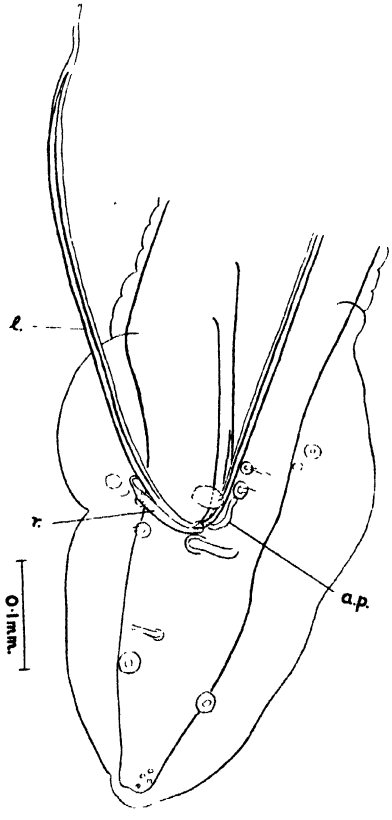


FIG. 12.—*Parabronema bonnei*. Posterior end of male; ventral view. *a.p.*, accessory piece; *l.*, left spicule; *r.*, right spicule.

The body-cavity of the present specimens, more especially of the females, contains large numbers of granules and globules of various sizes, which render it difficult, even after clearing in creosote, to distinguish the internal structures clearly. In the two males there are also curious amoeba-like masses of globules, with distinct outlines, lying within the caudal alae. It seems possible that these may be Protozoan parasites.

SKRJABINOFILARIA SKRJABINI Travassos, 1925.

Syn. *Cortiamosoides philanderi* Foster, 1939.

This species was obtained on five occasions from the pericardium of *Marmosa cinerea* near Paramaribo, in February and March, 1938. In two animals, according

to the collector's notes, the worms were 'mostly bundled up by aorta on dorsal side of heart'; in others 'mostly round heart'. One female worm is said by Mr. Sanderson to have measured 182 mm. in length. The length of the female is given by Travassos (1925) as 100 mm., and by Foster (1939) as 86–150 mm. Travassos records this species from the 'subcutaneous tissue of the ventral region' of *Didelphis opossum* in the State of Rio de Janeiro, Brazil. Foster describes what is unquestionably the same worm from the body-cavity of the Woolly Opossum, *Philander laniger pallidus*, in Panama. Travassos considers the genus closely related to *Setaria* and *Papillosetaria*. Foster considers it most closely allied to *Litomosoides* Chandler, 1931.

ACANTHOCEPHALA.

PROSTHENORCHIS ELEGANS (Dies., 1851).

This species was collected on five occasions from the intestine of *Saimiri sciurea*, and once from *Mystax midas*, in Surinam. According to Mr. Sanderson's notes, the worms were usually found in the large intestine, but occasionally in the small intestine. In one instance, when the host (*Saimiri*) had been dead at least five hours, he states that the worms were probably in the caecum during life. One was found in the caecum, one just below it in the large intestine, and one immediately above, at the extreme end of the small intestine. 'This monkey had been kept alive for three months and was subject to slight fits, becoming unconscious for a few minutes and foaming slightly at the mouth. It also seemed to suffer from a furious irritation of the lower belly. This it scratched until hairless and raw. It was immediately above the spot where the worms had resided'. Mr. Sanderson further remarks that the external surface of the caecum and of the upper 1½ cm. of the large intestine was marked with jet-black spots, which penetrated to the inner side. It seems possible that these marked former sites of attachment of the worms. In some portions of intestine preserved with the worms still attached, the anterior ends of the worms were deeply embedded in the tissues and surrounded by dense nodules which almost reached the outer coat.

The worms attain a considerably larger size than has hitherto been recorded for this species. Meyer (1932) states that the female is 18–25 mm. long, and the male somewhat smaller. In the present collection one specimen measures about 60 mm., and another about 70 mm., in length. Mr. Sanderson's notes mention more than once that these worms were of a blue colour, at least in their posterior portion, when alive, and in one case that they were bright blue with yellow extremities.

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Some Roundworms and Flatworms from the West Indies and Surinam.—II. Cestodes.

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(With 7 Text-figures.)

[Read 8 May 1947.]

This paper deals with five species of Cestodes collected by Mr. Ivan T. Sanderson at or near Paramaribo, Surinam (Dutch Guiana), in 1938. The type material of the new species described is in the British Museum (Natural History). The following is a classified list of the Cestodes included in the collection, with their hosts:—

	Host.
Diphyllobothriidae.	
Diphyllobothrium trinitatis Cameron, 1936.	Euprocyon cancrivorus.
Proteocephalidae.	
Proteocephalus appendiculatus, sp. n.	Tupinambis nigropunctatus.
Anoplocephalidae.	
Bertiella ? mucronata (Meyner, 1895) (fragments).	Cebus ? fatuellus.
Davaineidae.	
Raillietina (R.) alouattae, sp. n.	Alouatta macconnelli.
Dilepididae.	
Dipylidium caninum (L., 1758) (gravid segments).	Domestic dog.

Diphyllobothrium trinitatis Cameron, 1936.

A large number of specimens which are assigned to this species occurred in the upper two-thirds of the intestine of a Crab-eating Raccoon (*Euprocyon cancrivorus*) near Paramaribo. *D. trinitatis* was originally described from the same host in Trinidad, West Indies (Cameron, 1936). Professor T. W. M. Cameron has kindly presented some of the type specimens to the British Museum (Natural History), and these have been compared with the present material.

The specimens in the present collection measure up to about 35 mm. in length and 2-2·6 mm., or exceptionally 3 mm., in maximum width. Professor Cameron's specimens are said to have reached a length of 10 cm., but the longest of the co-types available measures about 52 mm. A few details may be added to the description. The length of the scolex varies from about 0·75 to 1·3 mm., according to age and state of contraction. In the original description a "neck" is stated to be absent. There is, however, in some specimens a very short region behind the scolex in which segmentation is not recognizable. The total number of segments in the strobila may be anything up to about 105 (or about 115 in the 52 mm. specimen). Genital rudiments begin to appear at about the 35th–45th segment. The number of testes per segment appears, at a very rough estimate, to be about 250. The cirrus-sac is almost spherical, but its transverse diameter is sometimes a little greater than its antero-posterior diameter (0·16–0·19 mm. as against 0·12–0·18 mm.). In Prof. Cameron's 52 mm. specimen a measurement of about 0·25 mm. in each direction was obtained, but the muscular wall of the sac may have been exceptionally relaxed in this case. In the original description it is stated that the two lateral fields of vitellaria do not meet in front of the genital pores. This may be true for segments in which the vitellaria have not yet reached full development, but in fully mature segments these glands are distributed evenly almost everywhere except in the central area occupied by the cirrus-sac, genital pores and uterus.

The uterus forms a very small mass relatively to the whole segment, even when packed with eggs, and appears to have usually only one loop on one side of the middle line, and two on the other. The eggs, after restoration of their normal contours by soaking in lactophenol, measure, in the Surinam material, 58–62 $\mu \times 30$–32 μ. In a Trinidad specimen they were found to attain a somewhat larger size (58–64 μ, or exceptionally 70 μ, in length and 36–40 μ in width ; the greater relative width giving them a somewhat rounder outline).

Among the Surinam specimens there occurred many immature, but segmented, specimens, and also three fragments, probably representing two specimens, of a much larger *Diphyllobothrium*. The longest of these fragments measured about 85 mm. in length and 4 mm. in width, and had a scolex about 2 mm. long. One of the other fragments was an anterior portion which had lost its scolex. The anatomy of all these fragments was abnormal, in that every mature segment contained from two to seven cirrus-sacs, arranged in a longitudinal series, and in many of them there were two or even three uteri containing eggs. A similar abnormality has been recorded by the writer (1945) in specimens believed to belong to the avian species *Diphyllobothrium dendriticum* that had developed in experimental mammals. It seems possible that in the present case the host had accidentally acquired an infection with a species which was ill adapted to it, and that in consequence the parasites had developed abnormally.

PROTEOCEPHALUS APPENDICULATUS, sp. n. (Figs. 1–4.)

This species occurred in the small intestine of the lizard *Tupinambis nigropunctatus* near Paramaribo. Specimens mounted in balsam measure 6–19 mm. in length, and have a maximum width of 0·4–0·7 mm. A complete strobila consists of only 9–16 segments, of which the last 2–8 are gravid. All except the youngest segments are longer than broad, and gravid segments attain a length of 2·5 mm. Rudiments of the genital organs are present in the youngest recognizable segments. There is only a very short unsegmented " neck ", varying, according to the size and state of contraction of the specimen, from about 0·15 to 0·4 mm. in length and from 0·35 to 0·7 mm. in width.

The cuticle is thin, and appears to be without spines or scales, even on the scolex. The musculature of the strobila is relatively weak. The main longitudinal muscles seem to consist of some 15 loose bundles of fibres dorsally and a similar number ventrally. There are two longitudinal excretory canals on each side. In mature segments these are in close apposition to the vitellaria, which lie between them. No transverse vessels have been detected.

The width of the scolex is 0·6–0·85 mm. It may be either somewhat conical at the apex (fig. 1) or assume a flattened form (fig. 2), in which case the suckers face anteriorly. There is no apical sucker, nor are there, apparently, any apical glands. The suckers are of an unusual and characteristic shape, each having a rounded anterior prolongation instead of being circular. When seen from the front (fig. 3), the apical region of the scolex forms a slightly raised disc measuring up to about 0·5 mm. in diameter and having a faintly lobate margin. There are four main lobes, alternating with the suckers and each divided into two by a slight indentation. The anterior prolongations of the suckers project into the disc between the main lobes. The musculature of the suckers does not appear to be very powerful, and in most of the specimens (fig. 2) it is relaxed, so that the suckers become almost flat discs. In this condition the prolongations appear solid, and show no evidence of being distinct locull or accessory suckers. Sections of some specimens (fig. 4, A), however, indicate that the main mass of the sucker and its prolongation are capable of forming separate cavities, so that each sucker may either be regarded as biloculate or as having a small accessory sucker on its anterior margin. The length of the suckers, including the prolongations, is about 0·3–0·35 mm. The width of the main part of the sucker is 0·19–0·3 mm., and that of the prolongation 0·1–0·13 mm.

The genital pores are irregularly alternating and at first situated at about the anterior third of the segment, but in the oldest gravid segments they are displaced backwards, sometimes almost as far as the middle. The cirrus-sac is sometimes anterior and sometimes posterior to the vagina in the same specimen. It is ovoid and measures about 0·2 mm. in length and up to 0·1 mm. in width. The cirrus is stout and apparently unarmed, and can be protruded to a great length. The vas deferens forms a rosette of coils before entering the cirrus-sac.

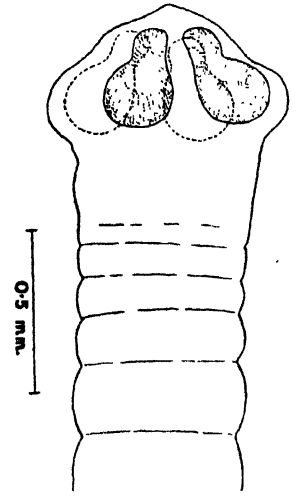
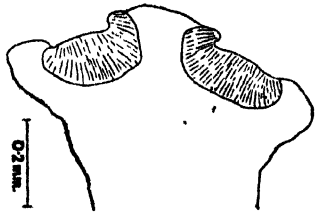


FIG. 1.—*Proteocephalus appendiculatus.* Scolex and anterior part of strobila; dorso-ventral view.



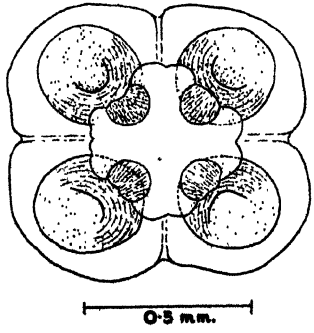


FIG. 2.—*Proteocephalus appendiculatus.* Horizontal section through scolex, passing through two of the suckers.

FIG. 3.—*Proteocephalus appendiculatus.* Scolex; frontal view.

The general anatomy of the segments is that typical of the family. The whole of the genital organs lie within the longitudinal muscles, i.e. in the medullary parenchyme. There are about 40–50 testes per segment. These are arranged on either side of the median uterus and across the anterior end of the segment. On the poral side they are divided into two groups by the genital ducts. The testes have a diameter of about 0·07 mm. when fully developed. The ovary is, as usual, situated at the posterior end of the segment and composed of two main lateral masses of follicles.

It is fully developed only in one segment before eggs appear in the uterus. It then measures about 0·3–0·4 mm. across, and occupies the whole width of the segment between the vitellaria. The latter are arranged in the usual manner, in two longitudinal bands laterally to the genital glands. The uterus appears early as a median longitudinal tube, and rapidly becomes filled with eggs. When it reaches its full development it has about 12–16 main lateral pockets on each side. The eggs are spherical and measure about 0·03 mm. in diameter. The onchospheres have a diameter of about 0·012 mm.

There is still no general agreement as to the taxonomy of the numerous genera and species of the Proteocephalid type. Some authorities (e.g. Fuhrmann, 1930–31) recognize two families, Proteocephalidae and Monticelliidae. Others (e.g. Woodland, 1933–35) regard the whole group as a single family, Proteocephalidae, and place *Proteocephalus* and its nearest allies in a subfamily Proteocephalinae (corresponding to the Proteocephalidae in Fuhrmann's sense), while a subfamily Monticelliinae and several other subfamilies have been erected, often for single genera, to take the place of the family Monticelliidae. There is also much divergence of opinion as to the definition of genera.

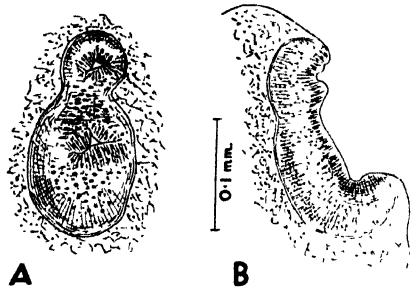


FIG. 4.—*Proteocephalus appendiculatus*. Sections through two suckers: A, horizontal section of a sucker in contracted condition; B, sagittal section of a relaxed sucker.

Whatever may be their relative merits, both of the main systems of classification depend upon the position of the genital glands with regard to the main longitudinal musculature of the strobila. In the Proteocephalinae (or Proteocephalidae *sensu stricto*) the testes, ovary and vitellaria all lie within this layer of muscles (i.e. in the medullary parenchyme), while in the other groups some or all of these organs lie outside it (i.e. in the cortical parenchyme). It is clear, therefore, that the present species must belong to the Proteocephalinae (or Proteocephalidae *s.s.*). There is, in fact, nothing in its structure to suggest that it is not a species of *Proteocephalus*, except the form of its suckers. In this one character, however, it shows a rather remarkable similarity to certain forms placed by Woodland in other subfamilies —*Peltidocotyle* Diesing, 1850 (Peltidocotylinae), *Amphoteromorphus* Dies., 1850, and *Zygobothrium* Dies., 1850 (Zygobothriinae). In the first two of these the suckers are biloculate, while in *Zygobothrium* each sucker has two apertures but only a single cavity. All these forms occur in fishes, and there is no reason for supposing that the somewhat similar form of the suckers in the present species represents more than a fortuitous convergence. It appears, however, to be unique among the Proteocephalids known from reptiles.

No cestodes of the Proteocephalid type seem to have been recorded from lizards of the family (Teiidae) to which *Tupinambis* belongs (see Hughes, Baker and Dawson, 1941). Of the dozen or more species described from Varanidae, all are of the '*Acanthotaenia*' type, having a covering of spines at least on the scolex. From other lizards, so far as the writer is aware, only three Proteocephalids have been recorded. *Proteocephalus* [*Acanthotaenia*] *striatus* (Johnston, 1914), from *Lialis*

burtonii in Australia, has simple suckers. The scolex of *P.* [*Crepidobothrium*] *amphiboluri* (Nybelin, 1917), from *Amphibolurus barbatus* in Australia, is unknown, but its strobila is clearly very different from that of the present species. A species of *Proteocephalus* is recorded by Harwood (1932) from *Anolis carolinensis* in Texas, but the specimen was immature and no description of it is given. A number of species of *Proteocephalus* (*sens. lat.*) have been recorded from South American snakes, but, in every case where the scolex is known, the suckers appear to be either of the typical, simple *Proteocephalus* form or else of the '*Crepidobothrium*' form, with an indentation in the posterior margin.

RAILLIETINA (RAILLIETINA) ALOUATTAE, sp. n. (Figs. 5–7.)

This species was found in considerable numbers on two occasions in the small intestine of howler monkeys (*Alouatta macconnelli*) near Paramaribo.

The length of preserved specimens is from about 130 to 340 mm., but when fresh the worms were evidently capable of much greater extension, as Mr. Sanderson's notes mention 'one, not stretched, 580 mm.'. The maximum width of the strobila varies between 2·5 mm. and 7 mm. The segments are mostly broader than long, though in specimens preserved in a well-extended condition the posterior (gravid) segments may be of about equal length and breadth.

The scolex measures about 0·45–0·62 mm. in width and about 0·38–0·47 mm. in dorso-ventral thickness. The rostellum has a diameter of 0·1–0·15 mm., and bears a total number of hooks estimated, in five specimens, at 176–224. These are arranged in two alternating crowns, and measure 15–17 μ in length. The greatest diameter of the suckers is 0·12–0·19 mm. They are armed with 10–12 rows of spines measuring 8–10 μ in length. There is a very short unsegmented 'neck', at first slightly narrower than the scolex, but segmentation begins at a distance of little more than 1 mm. from the anterior extremity.

The genital pores are all on the left side, and each is situated almost at the extreme anterior border of the segment. The main musculature of the strobila appears weak, the longitudinal muscles consisting of single fibres scattered throughout the thickness of the cortical parenchyme, without any definite arrangement in bundles or in layers. The transverse muscles also form a loose layer of single fibres at the junction of the cortical and medullary parenchyme. Numerous single dorso-ventral fibres pass right across the thickness of the strobila, and the usual subcuticular layers of transverse and longitudinal fibres are present. The lateral and transverse ventral excretory canals are relatively very wide. The dorsal canals are very narrow, and lie considerably nearer to the middle line of the strobila than the lateral ventral canals.

The genital ducts pass between the dorsal and ventral excretory canals, the vagina running parallel to the cirrus-sac and behind it. The cirrus-sac (fig. 6, *c.s.*) is pyriform and curved, with the concavity posterior. It measures about 0·22–0·25 mm. in length and 0·1–0·11 mm. in maximum width. Its inner end is swollen and somewhat constricted off from the distal portion, which is tapering. The whole organ is covered with a powerful muscular coat of criss-cross oblique fibres, the coat being thickest at the bulbous inner end. The cirrus (fig. 6, *c.*) is unarmed and of a very characteristic shape, being very short and expanded into a small bulb, which is prolonged on its anterior aspect into a narrow finger-like process curving posteriorly. The bulbous part of the cirrus-sac contains a widened and coiled portion of the vas deferens, functioning as an internal seminal vesicle. This duct narrows and straightens where it passes through the constricted region of the sac, and then, in the distal region, suddenly expands into a wider ejaculatory duct whose cuticular walls are lined with outwardly-directed spines. This tapers gradually to a narrow calibre before opening near the tip of the finger-like process of the cirrus. The portion of the vas deferens outside the cirrus-sac is narrow and coiled, and extends along the anterior border of the segment to the middle, enveloped throughout by a mass of gland-cells.

There are about 110–130 testes in each segment, forming a single layer and mostly arranged in a smaller poral group of about 30–40 and a larger aporal group of about 80–90, the two groups being joined by a few testes, usually in a single row, behind the female genital glands. On the poral side there are no testes in front of the vas deferens. The testes have a greatest diameter of 0·06–0·08 mm. when fully developed.

The distal part of the vagina, for a distance slightly greater than the length of the cirrus-sac, has a muscular wall, covered externally with gland-cells. This distal portion, like that of the vas deferens, has a cuticular lining armed with bristles pointing towards the exterior. At its proximal end it is suddenly constricted to form a short and very narrow duct. The rest of the vagina is a thin-walled tube which may be locally expanded at one or several places to form a temporary "receptaculum seminis". In the older segments, especially when gravid, the portion immediately following the constriction, and lateral to the ventral excretory canal, is very frequently distended with sperm, forming a fusiform expansion.

The ovary is slightly displaced towards the poral side of the segment, its aporal border being almost exactly in the middle line. It has two main lateral lobes, the whole forming a rosette with a width of about 0·3 mm. when fully developed. The vitelline gland, which lies behind the ovary, is subglobular and about 0·15 mm. wide. Dorsally to it lies the shell-gland. A small temporary uterus appears to be

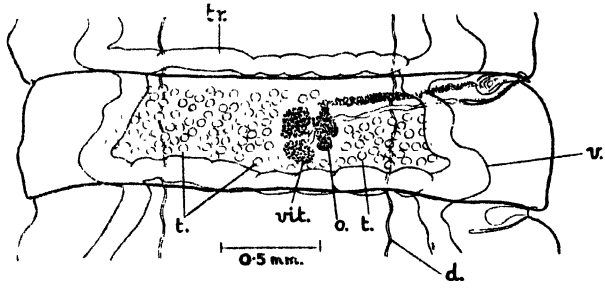


FIG. 5.—*Raillietina alouattae*. Mature segment; ventral view. *d.*, dorsal excretory canal, *o.*, ovary; *t.*, *t.*, testes; *tr.*, transverse excretory canal; *v.*, lateral ventral excretory canal; *vit.*, vitelline gland.

present just in front of the isthmus joining the lobes of the ovary. The eggs, however, almost immediately become scattered throughout the medullary parenchyme and enclosed in capsules. Of these there are about 38–55 in each gravid segment. They are usually confined to the space between the lateral ventral excretory canals, but occasionally a few occur dorsally and laterally to them.

The capsules are subglobular or ovoid, and have a greatest diameter varying between 0·15 mm. and 0·45 mm. Each capsule contains 6–11 eggs. These are also subglobular or ovoid, with a thin outer membrane measuring 0·04–0·06 mm. in maximum diameter. The onchospheres are spherical and have a diameter of 14–20 μ. Their hooks are about 5 μ long.

No species of the subgenus *Raillietina* appear to have been recorded from Primates other than man. From Lemuroids are recorded *R.* (*R.*) *lateralis* (Bourquin, 1906) (from *Galeopithecus*) and *R.* (? subgen.) *röthlisbergeri* Baer, 1935 (from *Nycticebus*). The forms recorded from man have been assigned by some authors to 13 * species, but these, according to López-Neyra (1943), can be reduced to four, thus :—

In the Ethiopian and Oriental regions :—

R. (*R.*) *formosana* (Akashi, 1916)—syns. *madagascariensis* of Garrison, 1911, *nec* Davaine; *garrisoni* Tubangui, 1931.

* The species *loechesalavezi* Dollfus, 1940, and *kouridovali* Dollfus, 1940, belong, according to López-Neyra, to the genus *Inermicapsifer*, and are synonyms of *I. cubanensis* (Kouri and Rappaport, 1939).

R. (*R.*) *madagascariensis* (Davaine, 1869)—syn. *davainei* Dollfus, 1940.

R. (*R.*) *celebensis* (Janicki, 1902)—syn. *asiatica* (Linstow, 1901).

In the Neotropical region :—

R. (*R.*) *demerariensis* (Daniels, 1895)—syns. *quitensis* León, 1935 ; *luisaleóni* Dollfus, 1939 ; *brumpti* Dollfus, 1939 ; *equatoriensis* Dollfus, 1939 ; *leoni* Dollfus, 1939.

R. formosana and *R. celebensis* are known also to occur in rodents, but it is curious that none of the other species have been found in any host but man. It is reasonable to suppose that man is no more than an accidental or occasional host, and that the normal hosts are wild mammals, possibly Primates, inhabiting the same geographical regions.

It might be expected that the present form would show closer affinities to *R. demerariensis* than to the old-world forms, and this appears, on the whole, to be the case. It differs from that species, however, in the same characters as from the others, viz. in having a greater number of testes and a smaller number of egg-capsules per segment, while the form and structure of the cirrus-sac and cirrus are quite distinctive. The following comparative table is based on data given by López-Neyra (1943) :—

	Number of rostellar hooks.	Number of testes.	Number of egg-capsules.
madagascariensis (incl. *davainei*)	unknown	ca. 50	90–180
celebensis (incl. *asiatica*)	80–120	28–50	60–150
formosana (incl. syns.)	90–140	26–59	150–400
demerariensis (incl. syns.)	152–200	40–86	70–350
alouattae	176–224	110–130	38–55

Note on the Development of the Terminal Genitalia in *R. alouattae*.

It is only in mature segments, in which the testes are beginning to be functional, that the cirrus is freely produced in the manner described above and illustrated in fig. 6. It seems doubtful whether, once protrusion has occurred, the cirrus can again be withdrawn. It has never been seen inverted within the cirrus-sac in the usual manner, and indeed it seems improbable that it can be so inverted. In examining strobilae prepared as whole mounts, it was observed that in all the fully-mature segments the cirrus was protruded, while in immature segments it lay within the genital atrium, and in close apposition to the opening of the vagina.

Horizontal sections of the appropriate region of the strobila reveal that the development of the cirrus actually takes place in the genital atrium, which, until this development is complete, has no opening to the exterior. In the earliest stage at which the cirrus is recognizable (fig. 7, A), it appears as a low papilla projecting into the atrium, which is continuous with the distal end of the vagina. The atrium is closed to the exterior by a wall of cuticle. The distal end of the vagina is, at this stage, a relatively wide tube without a lining of bristles or a definite muscular coat. The development of the bristles begins at the proximal end of what is eventually the muscular portion, and gradually proceeds distally. In slightly older segments (fig. 7, B) the papilla representing the cirrus projects further into the atrial cavity, which is still closed. In still older segments (fig. 7, C) the cirrus fills the whole of the atrial cavity (by which it seems, as it were, to be moulded into shape) and blocks the opening of the vagina. Its terminal finger-like process has not yet appeared, and the distal end of its duct is not in apposition to the vagina *. The cuticular membrane closing the atrial cavity is now ruptured—possibly as a result of the

* In the segment immediately behind that figured here, the cirrus was protruded and had a finger-like process.

expansion of the cirrus. The distal part of the vagina is now lined with bristles throughout, but appears much shorter and wider than when fully developed (cf. fig. 6). The bristles lining the ejaculatory duct are not yet visible.

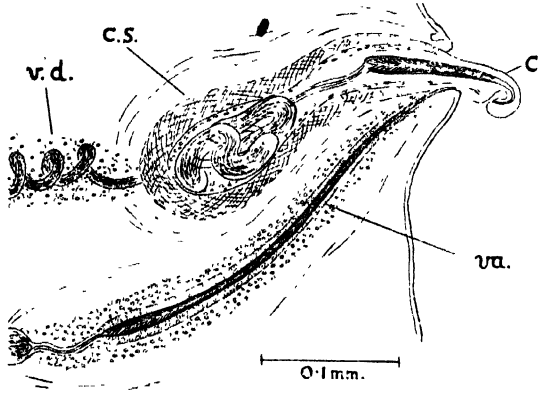


FIG. 6.—*Raillietina alouattae*. Reconstruction of cirrus-sac and vagina in a mature segment, from horizontal sections. *c.*, cirrus; *c.s.*, cirrus-sac; *va.*, vagina; *v.d.*, vas deferens.

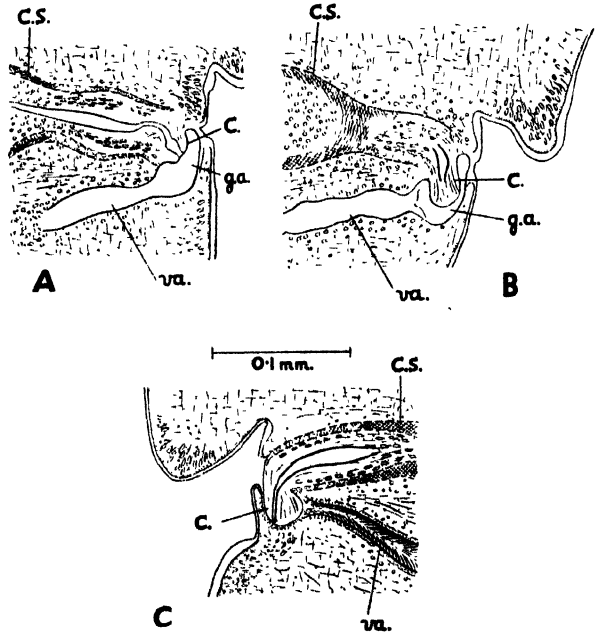


FIG. 7.—*Raillietina alouattae*. A, B, C, horizontal sections through terminal portions of cirrus-sac and vagina, showing three successive stages in development. *c.*, cirrus; *c.s.*, cirrus-sac; *g.a.*, genital atrium; *va.*, vagina.

There is here no question of self-fertilization, for the testes are not as yet fully developed and no spermatozoa are present. Dollfus (1940) has figured the cirrus and vagina in the position of 'autofécondation' in the closely-related forms *R. luisaleóni*, *R. brumpti*, *R. equatoriensis* and *R. leoni*—all, according to López-Neyra

(1943), synonyms of *R. demerariensis*. It is not stated whether this condition was observed in fully mature or immature segments. Some of the examples figured by Dollfus (figs. 13, 19) have the appearance of genuine cases of self-fertilization, for the cirrus is shown as inserted well into the vagina. In others, however, (figs. 22, 26), the appearance is more comparable with that described here, and a membrane is shown closing the genital atrium.

In certain of his figures (1940, figs. 23, 26) Dollfus has shown rounded bodies lying in the lumen of the vagina and of the ejaculatory duct, though no mention appears to be made of these bodies in the text. In some of the writer's preparations of *R. alouattae* masses of amorphous brownish material, sometimes quite spherical, sometimes elongated, occur in both these situations. They have been seen only in immature segments, and it seems possible that they may be coagulated droplets of the secretion of the cells concerned in forming the cuticular linings of the ducts.

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Some Roundworms and Flatworms from the West Indies and Surinam.—III. Trematodes. By STEPHEN PRUDHOE, Department of Zoology, British Museum (Natural History). (Communicated by Dr. H. A. BAYLIS, F.L.S.)

(With 2 Text-figures.)

The Trematodes recorded in this paper form part of a collection of parasitic worms from mammals and reptiles, obtained in the neighbourhood of Paramaribo, Surinam (Dutch Guiana), by Mr. Ivan T. Sanderson in 1938. For the privilege of studying these Trematodes the writer is indebted to Dr. H. A. Baylis, who has dealt with the Cestodes, parasitic Nematodes and Acanthocephala in the first two parts of the present series of papers.

PLAGIORCHIIDAE.

STICHOLECITHA SERPENTIS, gen. nov., sp. nov. (Figs. 1 & 2.)

Several examples of this species were found attached to the lining of the oesophagus of a snake, *Chironius carinatus*.

The body is somewhat boat-shaped, varying between 5·2 mm. and 8·4 mm. in length and between 1·2 mm. and 2 mm. in maximum width. In transverse section the anterior region is more or less circular, while the remainder of the body is flat or slightly concave ventrally and raised into a keel dorsally, as shown in fig. 2. This unusual shape is to be seen in all the present specimens, which were probably killed in formalin. The cuticle is thin and armed with sharply-pointed spines, each of which measures about 32 μ in length and about 10 μ in width at the base. These spines are very closely set anteriorly, but diminish gradually in number towards the posterior region of the body, and finally disappear before the hinder extremity. In some specimens the spines appear to have fallen off, leaving the body entirely smooth.

The oral sucker is subterminal and rounded or somewhat squarish in outline, measuring 0·56–0·65 mm. in diameter. The ventral sucker, which is situated at about the junction of the first and second thirds of the total length of the body, is a little smaller than the oral sucker, and measures 0·45–0·6 mm. in diameter. A short prepharynx, sometimes difficult to make out owing to contraction, opens into a well-developed, more or less rounded pharynx, which measures 0·21–0·25 mm. in diameter. The oesophagus varies between 0·2 mm. and 0·5 mm. in length. Numerous glandular cells lie in the parenchyme around the pharynx and oesophagus, and apparently open into the lumen of the latter, the lining of which appears to be cuticular. The intestinal bifurcation is situated about midway between the suckers. The intestinal caeca extend posteriorly to the middle region of the body or a little beyond, and are provided with a tall glandular epithelial lining. The excretory pore is terminal. The excretory vesicle is Y-shaped, with a very long stem extending to about the anterior margin of the foremost testis, where it divides into two very short branches which run anteriorly as far as the ovary.

The genital pore lies ventrally at or near the left margin of the body, a little anteriorly to the ventral sucker. It leads into a shallow atrium, at the base of which the openings of the cirrus-sac and metraterm lie side by side. The cirrus-sac is club-shaped and relatively long, extending transversely to the median line, where it lies immediately in front of the ventral sucker. Its wall appears to consist of a relatively thin layer of longitudinal muscle-fibres. The swollen proximal portion of the cirrus-sac contains a long, coiled seminal vesicle, which opens into a narrow pars prostatica surrounded by numerous prostate glands. The retracted cirrus is thick-walled and

unarmed. The testes are arranged one behind the other, either directly or obliquely, in the middle region of the body. They are rounded or somewhat oval, the anterior (0·5–0·75×0·45–0·5 mm.) being a little larger than the posterior (0·4–0·5×0·46–0·48 mm.). The ovary lies in the median line either dorsally to, or immediately behind,

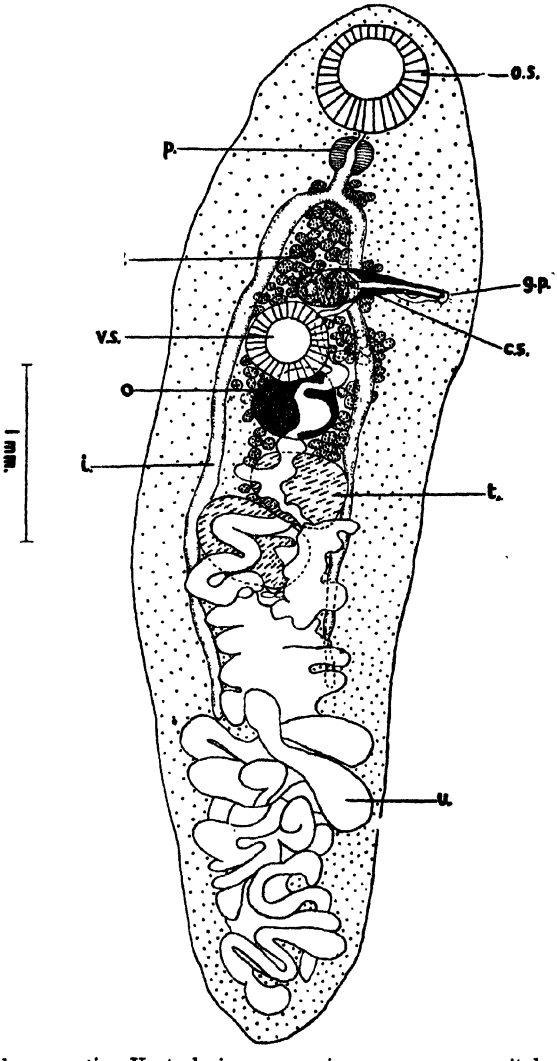

FIG. 1.—*Sticholecitha serpentis*. Ventral view. *c.s.*, cirrus-sac; *g.p.*, genital pore; *i.*, intestinal caecum; *o.*, ovary; *o.s.*, oral sucker; *p.*, pharynx; *t.*, testis; *u.*, uterus; *v.*, vitelline follicles; *v.s.*, ventral sucker.

the ventral sucker. It is rounded (0·48–0·5 mm. in diameter) or transversely oval (0·45×0·3 mm.). The oviduct begins on the right margin of the ovary, and runs posteriorly for a short distance, where a receptaculum seminis opens into it. At this point the oviduct turns ventrally to enter the oötype, into which open numerous

relatively large "shell"-glands. The receptaculum seminis is very small, and, although it is readily seen in serial sections, the writer has been unable to make it out in whole preparations stained with Mayer's paracarmine, or double-stained with indigocarmine and paracarmine. From the receptaculum seminis, Laurer's canal takes a slightly sinuous course towards the right surface of the keel-like dorsal wall of the body, and opens to the exterior near the median line of that surface.

The vitelline glands are disposed in an elongate group of rounded or pear-shaped follicles, situated in the dorsal half of the body, and extending along the median field from the region of the intestinal bifurcation to the hinder testis or a little beyond. In lateral view, the follicles appear to be disposed in distinct groups, like bunches of grapes, arranged in a single row. Each of these groups opens independently by a canal into a longitudinal yolk-duct, which lies in the median line, ventrally to the follicles. In most digenetic trematodes the vitelline follicles open into a pair of transverse yolk-ducts, and, since these are absent in the present form, it may be supposed that they are represented by the anterior and posterior ducts, which unite in the region of the ovary and open into a moderately long common vitelline duct. The latter appears to enter the oviduct without forming an enlarged vitelline

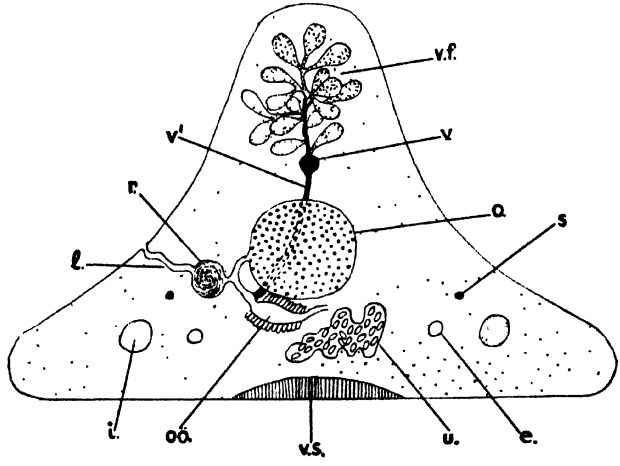

FIG. 2—*Sticholecitha serpentis*. Transverse section at level of ovary (diagrammatic). *e.*, branch of excretory vesicle; *i.*, intestinal caecum; *l.*, Laurer's canal; *o.*, ovary; *oö.*, oötype; *r.*, receptaculum seminis; *s.*, vas efferens; *u.*, uterus; *v.*, longitudinal yolk-duct; *v'.*, common vitelline duct; *v.f.*, vitelline follicles; *v.s.*, ventral sucker.

reservoir. The uterus is well developed, disposed in numerous transverse and dorsal loops, situated between the intestinal caeca, and extending into the sublateral fields of the body behind the caeca. In general, the loops of the descending portion of the uterus appear to lie on the right, and those of the ascending portion on the left side of the median line. The metraterm possesses a thin wall, and lies more or less along the dorsal margin of the cirrus-sac. Immediately before opening into the genital atrium, the dorsal half of the metraterm is provided with a very thick coat of muscle-fibres, which probably functions as a sphincter controlling the deposition of the eggs, as the lumen of the metraterm in this region is just sufficiently wide to allow the eggs to pass singly into the genital atrium. The eggs are operculate, and measure 0·025–0·027 × 0·012–0·015 mm. In the metraterm and distal portion of the uterus, the eggs appear to contain fully-formed miracidia.

During recent years the classification of the genera belonging to the family Plagiorchiidae (=Lepodermatidae) has been discussed by many writers. Some

(*e.g.* Mehra, 1937) regard the group as a single large family, consisting of some seventy or more genera, arranged in numerous subfamilies, while others (*e.g.* McMullen, 1937) treat it as a superfamily Plagiorchioidea, including several families.

The curious form described above is here provisionally assigned to the family Plagiorchiidae, *sensu lato*. The unusual shape of the body and the arrangement of the vitelline follicles enable this form to be readily distinguished from all other members of the family, although, at the moment, the shape of the body should only be regarded as a doubtful character, since it is questionable whether it is a normal feature during life, or has been brought about by contraction during fixation. In almost all Plagiorchiidae the vitelline follicles are situated in the lateral regions of the body, but in many species they are confluent in the median line anteriorly and posteriorly. In some species of *Opisthogonimus* Lühe the follicles may be disposed in two very indistinct groups, lying dorsally between the intestinal caeca in the middle region of the body. The general morphology of this genus, however, differs considerably from that of the present species. It is proposed, therefore, to erect for the latter a new genus, which may be defined as follows :—

STICHOLECITHA, gen. nov.

Plagiorchiidae. Body elongate. Suckers well developed; ventral sucker anterior to middle of body. Intestinal bifurcation midway between suckers. Excretory pore terminal; excretory vesicle Y-shaped, with long stem and short branches. Genital pore on, or near, left margin of body, immediately anterior to ventral sucker. Cirrus-sac club-shaped, extending transversely to median line; vesicula seminalis long and coiled; cirrus unarmed. Testes arranged one behind the other, tandem or obliquely, in middle region of body. Ovary lying dorsally to, or immediately behind, the ventral sucker. Receptaculum seminis very small; Laurer's canal present. Vitelline follicles disposed dorsally in an elongate group along the median line, extending from the intestinal bifurcation to the region of the hinder testis. Uterus voluminous. Eggs small and very numerous. Genotype : *S. serpentis*, sp. nov.

The type-material is in the British Museum (Natural History).

MICROPHALLIDAE.

MICROPHALLUS sp.

A single specimen of a species of *Microphallus* Ward, 1901, was found by Dr. Baylis in sediment from a tube containing a small portion of the intestine of an opossum, *Marmosa cinerea*. A careful examination of this portion of intestine unfortunately failed to reveal further specimens. At present, therefore, no direct evidence is available to show that this species of opossum is a normal host of a species of *Microphallus*.

The following is a brief description of the specimen :—Body broadly pyriform. Length 0·57 mm., maximum width, 0·47 mm. Cuticular spines sharply-pointed and very closely set anteriorly. Oral sucker $75\mu \times 92\mu$; ventral sucker $75\mu \times 87\mu$. Pharynx transversely oval, $24\mu \times 40\mu$; oesophagus and intestinal caeca were not made out. 'Genital papilla' 75μ in diameter. Large seminal vesicle dorsal to ventral sucker. Testes symmetrically arranged, more or less rounded, about 0·12 mm. in diameter. Ovary immediately in front of right testis, level with ventral sucker, rounded, 0·10 mm. in diameter. Vitelline follicles arranged in compact groups, ventrally to testes. Eggs 0·020 × 0·012 mm.

In a revision of the genus *Microphallus*, of which *Spelotrema* Jägerskiöld, 1901, and *Monocaecum* Stafford, 1903, are regarded as synonyms, Baer (1944) has assigned fourteen species to the genus. The present form differs from all these species in the position of the seminal vesicle, in that of the vitelline follicles and their distribution in relation to the testes, and in a few other minor points. It may possibly represent

a new species, but until further material becomes available, and allows a fuller description to be given, it seems preferable to regard the specimen as an indeterminate form of *Microphallus*.

PARAMPHISTOMATIDAE.

CLADORCHIS PYRIFORMIS (Diesing, 1836).

Numerous specimens collected from the duodenum of *Dasyprocta agouti* are provisionally referred to this species, which appears to have been recorded hitherto only from the caecum of the tapir (*Tapirus terrestris* [= *americanus*]) in Brazil. The worms are contracted, particularly in the anterior region of the body, and the few features in which they differ from *C. pyriformis*, as redescribed by Fischoeder (1903), are not considered to be of specific importance, since most of them are probably due to contraction. Furthermore, the different host-species may also have produced slight variations in the morphology of the worm. The following brief description indicates the more important differences :—

The body is somewhat conical in shape, and varies between 4 mm. and 6 mm. in length (5 mm. and 12 mm. according to Fischoeder) and between 2 mm. and 2·8 mm. in maximum width, which occurs in the posterior region. The posterior sucker is terminal and measures 1·5–1·8 mm. in transverse diameter. It varies between two-thirds and four-fifths of the maximum width of the body. Judging from Fischoeder's description, the ratio in *C. pyriformis* appears to be about 1 : 3. In *C. asper* (Dies.), also known only from *Tapirus terrestris*, this ratio is about 4 : 5. The sucker in both species is highly muscular and, no doubt, capable of considerable expansion and contraction. Hence, its size in relation to the maximum width of the body probably has no value as a specific criterion. The absence of papillae on the external surface of the posterior sucker apparently provides the main character for distinguishing *C. pyriformis* from *C. asper*, and in this respect the present material agrees with the former species. The testes are more frequently arranged side by side, which appears to be the normal arrangement in *C. pyriformis*, but they may also be seen lying obliquely, or even directly, one behind the other. The eggs measure 0·132–0·145 × 0·072–0·075 mm. (0·145–0·156 × 0·072–0·080 mm., according to Fischoeder).

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Some Roundworms and Flatworms from the West Indies and Surinam.—IV. Land-Planarians. By STEPHEN PRUDHOE, Department of Zoology, British Museum (Natural History). (Communicated by Dr. H. A. BAYLIS, F.L.S.)

(With 9 Text-figures.)

This paper, the last of the present series, deals mainly with seven species of land-planarians collected by Mr. Ivan T. Sanderson in the West Indies in 1937 and in Surinam (Dutch Guiana) in 1938. In addition, some account is given of the copulatory apparatus of *Amblyplana cockerelli* Graff, based on serial sections from one of the type-specimens, and a classified list, as complete as possible, is given of the Rhynchodemidae known to occur in the Americas.

The type-material belonging to Mr. Sanderson's collection is in the British Museum (Natural History).

GEOPLANIDAE.

GEOPLANA GIGANTEA Graff, 1899. (Fig. 1.)

This large species is represented by four specimens found in decaying logs and among damp leaves on Mount Aripo, Trinidad. Two of the specimens are mature and measure up to 18·5 cm. in length and 13 mm. in maximum width, while the others are immature and measure about 5 cm. and 5 mm. respectively. The body tapers to a blunt point at each end. It is dorso-ventrally flattened and measures about 2 mm. in maximum thickness in the larger specimens. In life, according to the collector's notes, the planarians were " rich flesh pink, yellow below, two brown stripes in anterior region." After preservation in alcohol for about ten years, the dorsal surface is now

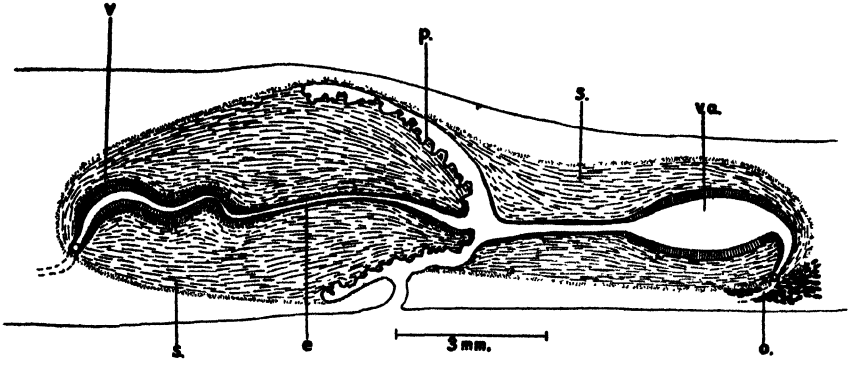

FIG. 1.—*Geoplana gigantea.* Sagittal section of copulatory complex (diagrammatic). *e.*, ejaculatory duct; *o.*, oviduct, with extracapsular gland-cells; *p.*, penis-papilla; *s.*, muscular sheath; *v.*, prostatic vesicle; *va.*, vagina.

yellowish brown, with a pair of submedian, purplish brown longitudinal stripes which are confined to about the anterior fourth of the body. Between the stripes the body is raised into a prominent ridge, which disappears near their posterior ends. The " creeping sole " is pale yellow-brown and apparently extends over the entire ventral surface. The mouth is situated somewhat behind the middle of the body and the genital pore is nearer to the mouth than to the posterior extremity.

The numerous eyes are confined to the anterior third of the body, and in the foremost region they are small and densely arranged in a narrow band on both lateral margins. As the bands extend posteriorly they gradually widen well into the sub-lateral regions beneath the dorsal surface and then narrow towards their hinder ends. Correspondingly, the eyes become larger, then smaller and less crowded.

The longitudinal fibres of the subepidermal musculature are arranged, as is usual in *Geoplana*, in distinct bundles which appear dorso-ventrally elongate in cross-section. In the parenchyme, just beneath the dorsal musculature, lie numerous unicellular glands, each of which contains several narrow fusiform rhabdites, measuring up to 32 μ in length.

The male and female copulatory organs are invested with an extremely thick muscular sheath, consisting of a thin outer coat of circular fibres and a very thick inner wall, mainly composed of longitudinal fibres. The sheath is somewhat bulbous in outline, and measures about 15 mm. in length and about 3 mm. in maximum width.

Numerous testes lie dorsally to the gut-branches. They appear to be arranged in four longitudinal rows, two rather close together on either side of the median line, and extending from the anterior region of the body to close behind the pharyngeal chamber. The vasa deferentia lie ventrally to the gut-branches and converge posteriorly towards the anterior end of the muscular sheath investing the copulatory organs. At this point they pass separately into the sheath and almost immediately unite to open into a prostatic vesicle. The latter is an elongate, somewhat coiled structure, provided with a highly glandular epithelium, which appears to be thrown into longitudinal folds, and its lumen contains a fine granular material, apparently produced by the epithelial cells.* The posterior end of the vesicle narrows gradually, and the thickness of its musculature diminishes considerably, before it merges with the ejaculatory duct. The duct is long and extends posteriorly to the tip of the penis-papilla. It has a very thin coat of circular muscle-fibres, and is lined with a smooth epithelium consisting of ciliated as well as glandular cells. The latter cells appear to contain a granular material rather similar in appearance to that present in the epithelial cells of the prostatic vesicle. The penis-papilla is large and muscular and its surface is much wrinkled, so that in section it appears to possess numerous small protuberances. It is covered by a low epithelium continuous with the lining of the spacious genital atrium.

There is a pair of ovaries in the anterior region of the body. The oviducts, lying laterally to the vasa deferentia, extend to the posterior end of the copulatory complex, where they open into the vagina. Numerous " shell "-glands lie outside the muscular sheath and open into the hinder regions of the oviducts. The elongate vagina is somewhat club-shaped and opens directly into the genital atrium. The lumen of its hinder half is much wider, and the epithelium taller and more glandular, than that of the anterior half. It might therefore be supposed that the spacious highly glandular portion was really the uterus, and the narrow less glandular region the vagina.

Geoplana gigantea has previously been recorded from the island of Trinidad, at Arima, the Vale of Marácas and the Ortoire Forest. It is also recorded by von Graff (1899) from Venezuela, at Carácas and on the banks of the Apure River, at an altitude of over 3,000 feet. His description of the coloration and markings of the body, as well as the distribution of the eyes, in the specimen from Carácas rather suggests, however, that he is dealing with a different species.

The original description of *G. gigantea* contains only details of external features, and nothing appears to have been known hitherto of the structure of the copulatory organs. According to von Graff, the longitudinal dorsal stripes extend throughout the length of the body. In all the present specimens the stripes are, however, found only in the anterior region. In the British Museum (Natural History) there is a mature specimen of *G. gigantea*, collected in Trinidad nearly fifty years ago, which agrees with

* A somewhat similar vesicle, usually regarded as a seminal vesicle, has been described in many species of *Geoplana*. The writer has been unable to find in the literature of the group any evidence showing that it actually functions as a sperm-reservoir. It seems that the vesicle is, in fully mature land-planarians, very often provided either with a highly glandular epithelium, or a ciliated epithelium through which pass the ducts of numerous extracapsular gland-cells. Both the glandular epithelium and the gland-cells undoubtedly produce the fine granular material frequently seen in the lumen of the vesicle. This material is very similar in appearance to the secretion seen in the prostatic organs of forms belonging to other groups of Turbellaria. Having regard to these observations, the writer prefers to consider the highly glandular organ in the present form as a prostatic vesicle rather than a seminal vesicle.

von Graff's description of the stripes and the darker ground-colour of the body, but otherwise does not appear to differ in any way from the present material.

Whether or not the present specimens from Trinidad should be regarded as representatives of a geographical race or variety of the mainland form is a question which could be settled only by a study of ample material from both regions.

GEOPLANA VAGINULOIDES (Darwin, 1844). (Fig. 2.)

The single specimen assigned to this species was collected from among damp leaves on Mount Aripo in Trinidad. It measures about 44 mm. in length and about 4 mm. in maximum width, which occurs in the middle region of the body. From its widest part the body tapers towards both extremities, more gradually anteriorly than posteriorly. The colour-pattern of the dorsal surface is very distinctive*. A broad, longitudinal median band of glossy black is bordered on either side by a narrower band of primrose-yellow, which is edged laterally with a narrow black stripe. All of these taper towards both ends, but none of them actually reaches the extremities. Finally, bordering the black stripes laterally, and extending over the extremities, is a relatively wide orange band. Ventrally, the whitish " creeping sole " lies between a pair of narrow orange bands which are really extensions of the dorso-lateral bands. The mouth is situated at about 25 mm. from the anterior end of the body and the genital pore about 5 mm. behind the mouth.

The numerous marginal eyes form a continuous series round the body. Anteriorly they are arranged more or less in a row, which gradually widens to a band several eyes deep in the pharyngeal region, but posteriorly the band narrows again to a row of widely-separated eyes.

The copulatory organs are invested with a muscular sheath, consisting of irregularly disposed fibres, except in the peripheral regions of the sheath, where they are mainly longitudinally arranged. The vasa deferentia pass separately into the anterior end of the sheath and soon unite to open into the rather long, coiled ejaculatory duct, which, like the vasa deferentia, is lined with a tall ciliated epithelium and covered with a moderately thick coat of circular muscle-fibres. In the anterior region of the muscular sheath lie numerous gland-cells, which apparently open into the lumen of the ejaculatory duct, near its proximal end. These gland-cells produce a fine granular material, which is stained a distinctive reddish brown by eosin. In appearance and in its reaction to eosin the granular material is very similar to the prostatic secretion of other Turbellaria, and this portion of the ejaculatory duct may function as a prostatic organ. A well-developed, somewhat elongate penis-papilla lies in a spacious male atrium. It appears to be coated with a glandular epithelium, beneath which lies a fairly thick layer of circular and a thinner supporting layer of longitudinal muscle-fibres. In the anterior region of the penis-papilla the external covering appears, however, to be merely an epithelial membrane, and the musculature is very thin. The difference in the thickness of the epithelium in different regions is doubtless due to the activity of its musculature.

The female complex does not appear to be fully developed. The oviducts are situated ventrally to the gut-branches, but well separated from the ventral musculature of the body-wall. In the neighbourhood of the genital atrium they rise steeply to open into the narrow " common glandular canal " which unites with the inner end of the vagina. The oviducts and the " common glandular canal " are lined with a ciliated epithelium and coated with circular muscle-fibres. " Shell "-glands and vitelline glands have not been made out. The vagina is bulbous and entirely filled with a mass of tissue, which has a vacuolated appearance and contains innumerable nuclei. This mass of tissue may possibly serve as a plug to prevent spermatozoa entering the female apparatus before the ovaries are ripe—only the posterior half of the present specimen has been sectioned, and therefore the condition of its ovaries is not known. It also seems possible that when the female apparatus becomes

* An excellent coloured figure of the dorsal aspect of this species is given by Reister (1938 pl. i, fig. 20).

functional the mass breaks down and forms the glandular epithelial lining usually present in the vagina of land-planarians. A distinct lining is not yet differentiated in the vagina of the present specimen. In the literature of the group there are records (e.g. Graff (1899 and 1916), and Reister (1938)) of the presence of a mass of material in the vagina of several species of *Geoplana*. In some of these instances (e.g. Graff) there can be little doubt that the masses represent cocoons, but in others (e.g. Reister) there is evidence that they are comparable with that seen by the writer. The covering of the cocoon in land-planarians is apparently formed by the secretion of the " shell "-glands, which is stained a distinctive reddish brown by eosin, and in the present specimen no part of the mass appears to have been similarly affected by this stain. In support of the suggestion as to the purpose of the mass of tissue in the present specimen, it is again mentioned that " shell "-glands and yolk-glands have not been made out, nor does there appear to be evidence of sperm in any part of the female complex. In fact, as stated above, the complex does not seem to be fully developed.

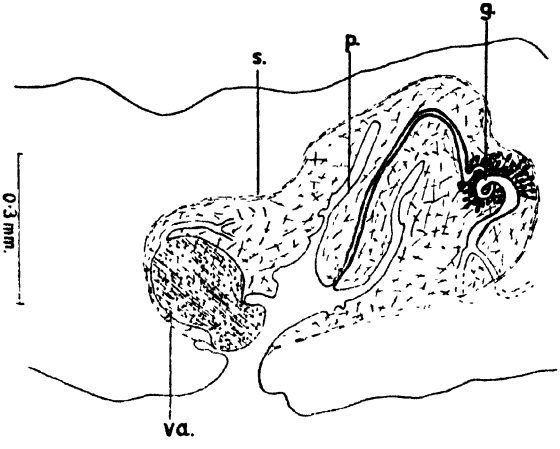

FIG. 2.—*Geoplana vaginuloides*. Sagittal section of copulatory complex (camera-lucida outlines). *g.*, glandular portion of ejaculatory duct ; *p.*, penis-papilla ; *s.*, muscular sheath ; *va.*, vagina.

On the other hand, de Beauchamp (1939) describes and figures a mass of tissue, apparently possessing a very narrow lumen, in the bursa copulatrix of *Geoplana crawfordi*, and the appearance of the mass is unquestionably comparable with that seen by the writer. In the two specimens at the disposal of de Beauchamp the "shell"-glands and yolk-glands are present, and that author records the presence of spermatozoa among the loose outer tissues of the mass in one of the specimens. de Beauchamp's types of *G. crawfordi*, which are in the British Museum (Natural History), have been carefully examined by the writer, but no evidence has been found of the presence of sperm in any part of the female complex of either specimen. It is worthy of mention that the vagina (or bursa copulatrix) of *G. crawfordi* does not appear to possess an epithelial lining which can be differentiated from the nucleated mass of tissue. Furthermore, the presence of a narrow lumen in the mass in *G. crawfordi* tends to support the writer's suggestion that the tissue breaks down and forms an epithelial lining for the vagina. Whether or not the so-called vagina or bursa copulatrix should not, in fact, be regarded as a uterus is a question that must be left in abeyance until more is known of the development of the structure.

Apart from the more advanced development of the female copulatory apparatus, Reister's (1938) description of the copulatory organs of *G. vaginuloides* differs from that given above principally in the size of the penis-papilla. According to that author, the penis-papilla in a quiescent state is very elongate and occupies the whole of the

vaginal cavity, and its narrow apex lies within the " common glandular canal." The entire occupation of the vagina by the " resting " penis-papilla of the same individual is, of course, very exceptional in land-planarians, and it is unfortunate that, although Reister apparently had ample material at his disposal, he omits to state whether or not the position of the penis-papilla in relation to the female apparatus is a normal feature in fully adult specimens of this species.

G. vaginuloides has been recorded hitherto only from Brazil, at Rio de Janeiro (type locality), Barreira and Therezopolis. However, the colour-pattern of the dorsal surface in *G. vaginuloides* is characteristic, and in this respect the specimen from Trinidad agrees so well with previous descriptions that the writer feels no hestitation in regarding it as conspecific with Darwin's species.

GEOPLANA SANDERSONI, sp. nov. (Figs. 3–5.)

A single specimen of this form was collected from among dead leaves on Mount Aripo in Trinidad. It is fairly slender, tapering towards the extremities, and measures about 28 mm. in length and about 3 mm. in maximum width. The dorsal surface is light brown, with a pair of submedian dark brown bands extending throughout the length of the body. The area between these bands is somewhat lighter in colour than the areas lateral to them. Ventrally, the very broad whitish ' creeping sole ' is bordered on either side by a light brown stripe. The mouth is situated at about 17 mm. from the anterior end of the body and the genital pore about 5 mm. behind the mouth.

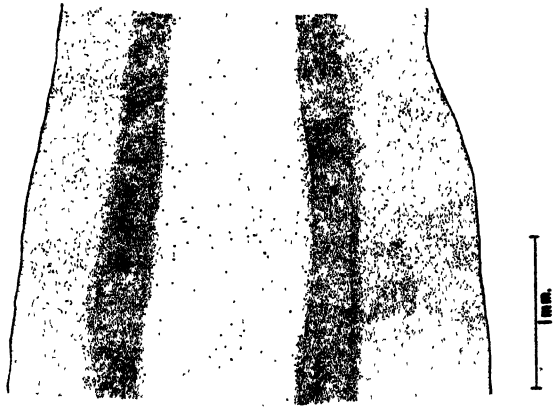

FIG. 3.—*Geoplana sandersoni.* Dorsal view of middle region.

The numerous marginal eyes are distributed in a continuous series round the body. Anteriorly they appear to be arranged in one or two irregular rows, but behind this region they form a band which gradually extends well into the sublateral fields beneath the dorsal surface. Posteriorly, however, the band narrows considerably to form a row of widely-separated eyes.

The entire copulatory apparatus does not appear to be invested with a muscular sheath, as in the previous species, but the musculature of the penis-papilla is very well developed and forms a thick coat of fibres round the seminal vesicle and ejaculatory duct. Behind the pharynx the testes are situated ventrally to the gut-branches, and the vasa deferentia lie above them, between the dorsal and ventral fields of the body, and between the pair of posteriorly-directed intestinal caeca. Near the genital pore the vasa deferentia turn inwardly towards the median line, where they open into a narrow seminal vesicle. The ejaculatory duct is very long, and instead of the

seminal vesicle or the vasa deferentia uniting with its anterior extremity, as is usual in *Geoplana*, the union occurs in the middle region of the duct, so that the latter possesses an anterior appendix. Both the ejaculatory duct and the seminal vesicle are lined with a ciliated epithelium, and coated with a relatively thick layer of circular muscle-fibres. There seems, in fact, to be no histological difference in the appearance of the two organs. The penis-papilla is elongate and strongly muscular. It is covered with an epithelial membrane, and lying in the musculature immediately below this there is a large number of small pyriform organs. Each of these organs possesses an outer sheath of muscle-fibres, and an inner mass of granular material in which there are numerous strands of tissue. In the narrow distal region of each organ lies a second pear-shaped structure or ampulla, the wall of which appears to consist of a thick membrane, perforated in its inner half by numerous ducts. It seems probable that the granular content of the main organ passes through these ducts into the lumen of the smaller organ. Several nuclei are present in the main organ and form a ring round the narrower half of the ampulla. It has not been possible in the present specimen to make out the relationships of these nuclei, but it is possible that they belong to cells which produce the granular material present in the main organ. The ampulla opens to the exterior by a very small pore on the surface of the penis-papilla. The function of these organs is at present unknown, but possibly they represent individual prostatic organs.

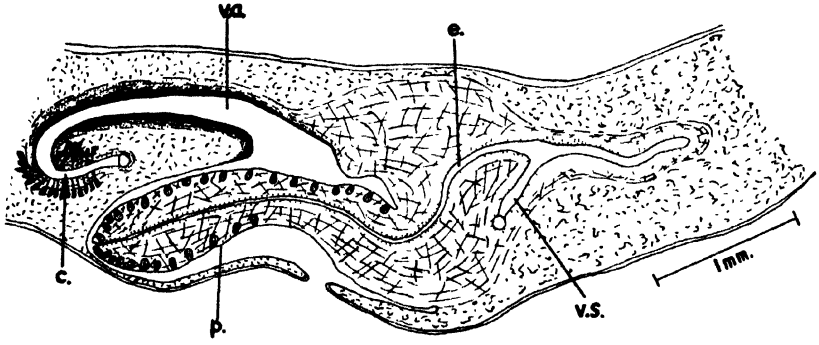

FIG. 4.—*Geoplana sandersoni*. Sagittal section of copulatory complex (camera-lucida outlines). *c*, 'shell'-chamber; *e.*, ejaculatory duct; *p.*, penis-papilla; *va.*, vagina; *v.s.*, seminal vesicle.

Close behind the genital atrium the oviducts, which are situated laterally to the vasa deferentia, unite to form a short posteriorly-directed "shell"-chamber or "common glandular canal," into the lumen of which open numerous unicellular glands or "shell"-glands. The canal turns sharply dorsally to open into the posterior end of the fairly long, wide vagina. The latter possesses a rather tall glandular epithelial lining, and is coated with a thick layer of circular muscle-fibres lying between two thin longitudinal layers.

The genital atrium is spacious and mainly occupied by the penis-papilla.

With the exception of *Geoplana von gunteri* Fuhrmann, 1914, from Colombia, the present form is distinguished from all known species of *Geoplana* Stimpson, 1857, in which the structure of the copulatory apparatus has been described, by the presence of the small pyriform organs lying in the walls of the penis-papilla. It differs from *G. von gunteri* not only in the colour-pattern of the dorsal surface of the body, but also in several features in the copulatory apparatus.

The structure of the pyriform organs shows a considerable resemblance to similar organs present in the male "adenochire" of *Artioposthia* Graff, 1896—especially *A. diemenensis* (Dendy). In this respect, the present species and *G. von gunteri* form

a group intermediate between *Geoplana* and *Artioposthia*, but otherwise both species appear to be typical members of *Geoplana*. It is possible, of course, that a more detailed study of these two species, based on further material, will show other features which, when correlated with the presence of special gland-organs in the penis-papilla, provide solid grounds for the erection of a new genus.

GEOPLANA sp.

A single immature specimen, tentatively assigned to the genus *Geoplana*, was collected at night on the surface of damp soil above Kaimanston in Surinam. It is, unfortunately, badly damaged, but some of its external characters may be mentioned.

The body is elongate, bluntly pointed anteriorly and rounded posteriorly. It measures about 60 mm. in length and about 2·5 mm. in maximum width. The dorsal surface possesses a narrow longitudinal median band of yellowish brown, which is bordered on either side by a dark brown band of similar width. Laterally to each submedian band there is a much wider yellowish-brown band which is rather darker than the median. The mouth is situated a short distance behind the middle of the body. Numerous marginal eyes appear to be arranged in one or two irregular rows, forming a continuous series round the body.

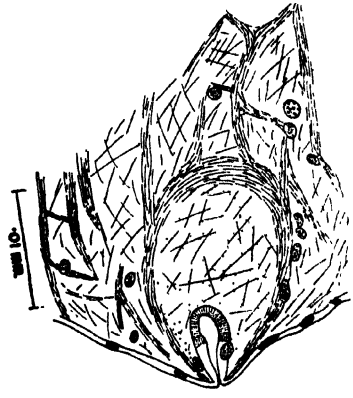

FIG. 5.—*Geoplana sandersoni*. Pyriform organ in wall of penis-papilla.

In coloration and markings this specimen closely resembles several species of *Geoplana* recorded from South America, but it has not been possible to assign it with certainty to any of them. A knowledge of the structure of the copulatory organs of the species is needed before its generic status can be determined with certainty, but until adult material from Surinam becomes available it may be regarded as an indeterminate species of *Geoplana*.

GEOPLANA sp.

A single specimen was found at the base of a tree at night on Mount Aripo in Trinidad. It is immature, and therefore can only be provisionally regarded as a species of *Geoplana*. The body measures about 20 mm. in length and about 3 mm. in maximum width, and tapers to a rounded point at the extremities. The dorsal surface is rather brownish black, except where the epithelium has been lost, and is without stripes or bands of any kind. The greyish white " creeping sole " occupies nearly the whole of the ventral surface, but is bordered by very narrow marginal bands of black. The mouth is situated at about 5 mm. from the posterior extremity.

The marginal eyes are very numerous and form a complete series round the body.

In the middle region they are arranged in a broad band extending into the sublateral zones beneath the dorsal surface, and anteriorly and posteriorly the band decreases in width to an irregular row of eyes, numerous anteriorly and sparsely distributed posteriorly.

Apart from *G. gigantea*, the only species of *Geoplana* that have been recorded hitherto from Trinidad appear to be *G. ehlersi* Graff, 1899, and *G. kenneli* Graff, 1899. In the general coloration of the body the present form shows some resemblance to *G. ehlersi*, but this species apparently possesses a conspicuous yellow median stripe on the dorsal surface, and appears also to have a much more slender body.

RHYNCHODEMIDAE.

Heinzel (1929) divides the Rhynchodemidae into two subfamilies : Desmorhynchinae, in which the longitudinal fibres of the subepidermal musculature are aggregated into distinct bundles ; and Rhynchodeminae, in which the longitudinal fibres of the musculature are arranged, not in bundles, but in a very thin simple layer. In the same paper, Heinzel selects *Planaria terrestris* Müller, 1774, as the genotype of *Rhynchodemus* Leidy, 1851. But Miss Hyman (1943) points out that the type of *Rhynchodemus* is *Planaria sylvatica* Leidy, 1851, and that in new material, which she considers to belong to Leidy's species, the longitudinal fibres of the subepidermal musculature are disposed in bundles, as in Heinzel's Desmorhynchinae. This fact leads her to regard *Desmorhynchus* Heinzel as a synonym of *Rhynchodemus* Leidy, and *Rhynchodemus* of Heinzel as a total synonym of *Geodesmus* Mecznikow, 1866. As Heinzel's subfamily names therefore become invalid, Miss Hyman proposes the name Dolichoplaninae for Desmorhynchinae, and Geodesminae for Rhynchodeminae. It appears to be implicit in Article 4 of the International Rules of Zoological Nomenclature that, when a family is divided into two or more subfamilies, the type-genus of the family must also become the type of one of the subfamilies. Hence the root of the generic name must be present not only in the name of the family, but in that of the subfamily. Consequently, if it be thought necessary to divide the Rhynchodemidae into two subfamilies, the name Geodesminae Hyman appears to be available for the Rhynchodeminae of Heinzel, and the writer suggests that the name Rhynchodeminae be retained in a new sense to include the Desmorhynchinae of Heinzel and the Dolichoplaninae of Hyman.

With regard to the Rhynchodemidae recorded from the Americas, it seems desirable to reclassify the known species, and a list of them, including the new forms described herein, is as follows :—

Subfamily RHYNCHODEMINAE, sens. nov. (*nec sensu* Heinzel, 1929).

(=Dolichoplaninae Hyman=Desmorhynchinae Heinzel.)

Genus RHYNCHODEMUS Leidy, 1851, *sensu* Hyman, 1943.

SPECIES.	DISTRIBUTION.
sylvaticus (Leidy, 1851).	U.S.A. (Rhode I., Pennsylvania, Ohio and Missouri).
hectori Graff, 1897.	Argentina (Provinces of Salta, Jujuy and Tucuman).
blainvillei Graff, 1899.	Brazil (Sa. Catharina Prov.).
pellucidus Graff, 1899.	Brazil (Sa. Catharina Prov.).
bromelicola de Beauch., 1912.	Costa Rica.
samperi Fuhrmann, 1914.	Colombia (Eastern Cordilleras).
angustus (Hyman, 1941).	Panama, Canal Zone (Barro Colorado I.).
americanus Hyman, 1943.	U.S.A. (greenhouses in Missouri and New Jersey).
aripensis sp. nov.	Trinidad (Mt. Aripo).
sp. de Beauch., 1939.	Peru (Capachica).
' sp. *A* ' Hyman, 1943.	U.S.A. (greenhouses, Washington, D.C.).
' sp. *B* ' Hyman, 1943.	U.S.A. (greenhouses, Missouri).

Genus DOLICHOPLANA Moseley, 1877.

SPECIES.	DISTRIBUTION.
striata Moseley, 1877.	U.S.A. (greenhouses, Missouri).
joubini Hallez, 1894.	French Guiana (Cayenns).
feildeni Graff, 1899.	Barbados, West Indies.
carvalhoi Corrêa, 1947.	Brazil (São Paulo).

Graff (1899) is of the opinion that *joubini* and *feildeni* are probably synonymous, and some recent authors appear to regard *feildeni* as a synonym of *striata*.

Subfamily GEODESMINAE Hyman, 1943.

(=Rhynchodeminae of Heinzel, 1929.)

Genus GEODESMUS Mecznikow, 1866, *sensu* Hyman, 1943.

SPECIES.	DISTRIBUTION.
cockerelli (Graff, 1899).	Jamaica, West Indies.
atrocyaneus (Walton, 1912).	U.S.A. (central States).
maculatus (Fuhrmann, 1914).	Colombia (Eastern Cordilleras).
montoyae (Fuhrmann, 1914).	Colombia (Eastern Cordilleras).
haitiensis, sp. nov.	Haiti (Mt. Commissar).

Genus DIPORODEMUS Hyman, 1938.

SPECIES.	DISTRIBUTION.
yucatani Hyman, 1938.	Yucatan.
plenus Hyman, 1941.	Panama, Canal Zone (Barro Colorado I.).
indigenus Hyman, 1943.	U.S.A. (Appalachian region).

Forms that cannot yet be classified with any degree of certainty are :—

SPECIES.	DISTRIBUTION.
Rhynchodemus (s. l.) *stenopus* Graff, 1894.	Argentina and Venezuela.
Rhynchodemus (s. l.) *borrellii* Graff, 1894.	Paraguay.
Rhynchodemus (s. l.) *costaricensis* de Beauchamp, 1913.	Costa Rica.

RHYNCHODEMUS ARIPENSIS, sp. nov. (Fig. 6.)

A few specimens of this species were found in the heads of bromeliads, sixty feet above ground-level, on Mount Aripo in Trinidad. They measure up to about 22 mm. in length and about 2 mm. in maximum width. The body tapers more gradually anteriorly than posteriorly. The dorsal surface is light brown, with three longitudinal stripes of equal width. The dark brown median stripe is always conspicuous, but the sublateral stripes are rather indistinct and cannot be seen in some specimens. For a distance of about one-eighth to one-seventh of the total length of the body, the anterior region is much lighter in general colour, and is without stripes. As in many other species of *Rhynchodemus*, this cephalic region is relatively narrow and distinctly marked off from the remainder of the body, having the appearance of an elongate snout or proboscis. Ventrally, the whitish " creeping sole " is slightly raised and occupies the middle third of the body-width. The lateral areas of the ventral surface are light brown. The mouth is situated in the middle region of the body and the genital pore about 4 mm. behind the mouth. Two relatively large eyes lie behind the anterior extremity of the snout-like region.

The longitudinal fibres of the subepidermal musculature are arranged in distinct bundles which appear oval in cross-section.

The numerous testes are disposed in two irregular rows, ventrally to the gut-branches. The male copulatory apparatus is simple and typical of the genus *Rhynchodemus*, *sensu* Hyman. It is contained in a thick sheath of muscle-fibres,

mainly longitudinal, representing the penis-bulb. The vasa deferentia pass separately through the anterior wall of the sheath and open together into a spacious atrium. This atrium, or ejaculatory duct, is lined with a highly glandular epithelium and coated with circular and longitudinal muscle-fibres. The parenchymatous tissue between the walls of the sheath and those of the atrium contains a loose irregular network of muscle-fibres, among the meshes of which lie numerous gland-cells.

The structure of the female copulatory apparatus is simple and agrees well with that usually present in *Rhynchodemus*. The oviducts lie ventrally to the gut-branches and laterally to the vasa deferentia. The vitelline glands are very numerous, lying between, as well as above and below, the gut-branches. At the posterior end of the apparatus the oviducts unite, apparently without bifurcating, to form a ciliated canal which enters a short, narrow " shell "-chamber. This chamber is also ciliated, and surrounding it are numerous " shell "-glands which open into its lumen. The vagina is elongate, but spacious, and possesses a highly glandular epithelial lining. The

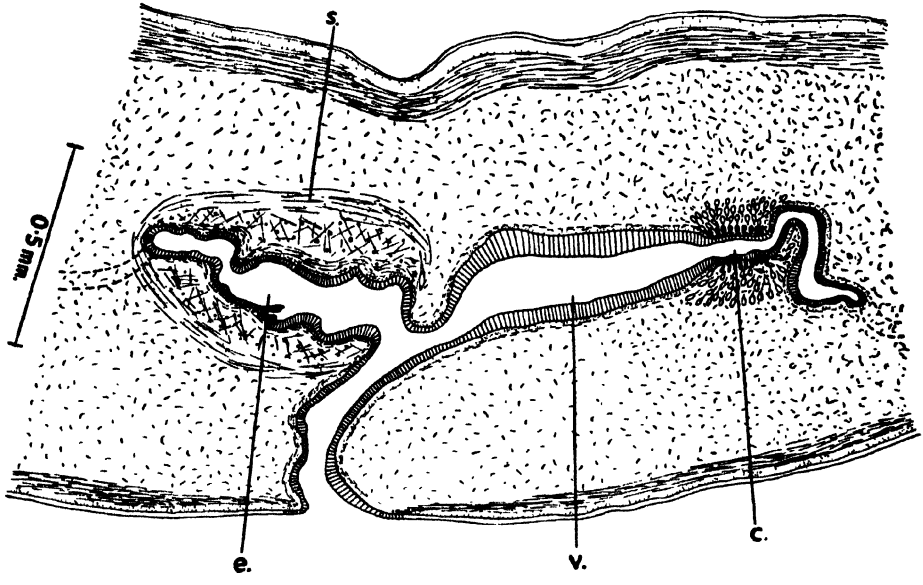

FIG. 6.—*Rhynchodemus aripensis*. Sagittal section of copulatory complex (camera-lucida outlines). *c.*, ' shell '-chamber ; *e.*, ejaculatory duct ; *s.*, muscular sheath ; *va.*, vagina.

apparatus is coated with a relatively thick inner layer of circular and a thin outer layer of longitudinal muscle-fibres. It appears to be as long as, or slightly longer than, the male apparatus.

Of the American Rhynchodemids that can at present be assigned with certainty to the genus *Rhynchodemus*, *sensu* Hyman, the species described above closely resembles *R. sylvaticus* (Leidy), *R. pellucidus* Graff and *R. samperi* Fuhrm. The first two of these species are, however, much smaller forms and each bears only two dorsal stripes on its body, while *R. samperi* is a more slender creature, its median dorsal stripe is much narrower than the lateral stripes, and the female copulatory apparatus appears to be considerably smaller than the male. It is therefore considered necessary to regard the form from Trinidad as a new species.

GEODESMUS HAITIENSIS, sp. nov. (Figs. 7 and 8.)

Two specimens of this form were found under the bark of a decaying log on Mount Commissar, Haiti. They are plump and elongate, circular in cross-section, and about

25 mm. in length and about 4·5 mm. in width. In life, according to the collector's notes, the body was : " Jet black. Edges (lateral) yellow ochre. Grey below." After about ten years in alcohol, the coloration of both specimens has only slightly faded. The dorsal surface is now greyish black. On each side of the body there is a wide yellow lateral band, which may be seen in either the dorsal or the ventral aspect. Anteriorly and posteriorly the yellow bands widen to enclose the extremities. Ventrally, the ' creeping sole ' is light grey and extends across the middle third of the body-width in different regions. It is bordered on either side by a wide band of black. The mouth is situated at about 17 mm. from the anterior end of the body and the genital pore about 4 mm. behind the mouth. The two eyes are comparatively small and appear to be dorso-ventrally elongate.

The subepidermal musculature is thin, and its longitudinal fibres are disposed in a simple layer. In the parenchyme, well separated from the subepidermal musculature, lie innumerable small bundles of longitudinal muscle-fibres, which are more numerous in the lateral than in the dorsal or ventral regions of the body. The bundles appear to form a sheath around the digestive and reproductive organs.

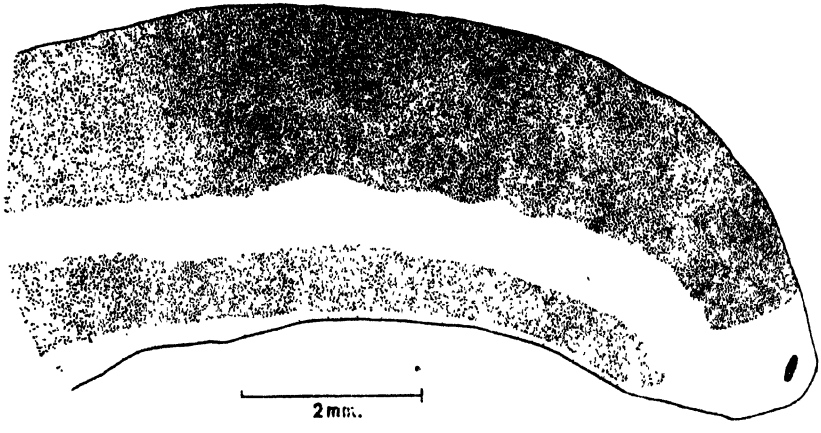

FIG. 7.—*Geodesmus haitiensis*. Lateral view of anterior region.

The male copulatory apparatus is invested with a thin sheath of longitudinal muscle-fibres, which encloses the parenchymatous network surrounding the copulatory organs. The vasa deferentia lie ventrally to the gut-branches. They pass into the antero-ventral wall of the sheath and open together into a rather wide ejaculatory duct. The duct takes a sinuous course posteriorly to the apex of the penis-papilla. It is coated with a thick inner layer of circular and a thin outer layer of longitudinal muscle-fibres, and lined throughout with an exceptionally tall glandular epithelium, the cells of which appear to contain a granular material. The nuclei of this epithelium are not abundant in the proximal or inner region of the duct. The penis-papilla is large and robust, and occupies the whole of the male atrium. It is covered with an epithelial membrane attached to an extremely thin basement-membrane. Beneath the latter lies a thick layer of tightly-packed muscle-fibres which are disposed at right angles to the surface of the penis-papilla. Numerous nuclei lie in the inner regions of the muscle-layer. Supporting this layer is a coat of longitudinal muscle-fibres, the thickness of which is about one-third that of the former. In the parenchymatous tissue, immediately around the ejaculatory duct, there is a fine granular material, rather similar in appearance to that seen in the epithelial lining of the duct.

The female copulatory apparatus is simple and lies in a sheath of mixed longitudinal and circular muscle-fibres. The oviducts open ventrally into a spacious ' shell '-chamber, situated in the posterior region of the sheath. The ' shell '-chamber is

lined with a tall glandular epithelium and surrounded by numerous gland-cells which open into its lumen. The vagina is spacious and lined with an epithelium continuous with that of the ' shell '-chamber. Inside the sheath, round the vagina, is a network of parenchymatous tissue which has a more compact appearance than that investing the male copulatory organs.

The present form may be readily distinguished from all the known species of *Geodesmus*, *sensu* Hyman, not only by the colour-pattern of the body, but also by the peculiar musculature of the penis-papilla.

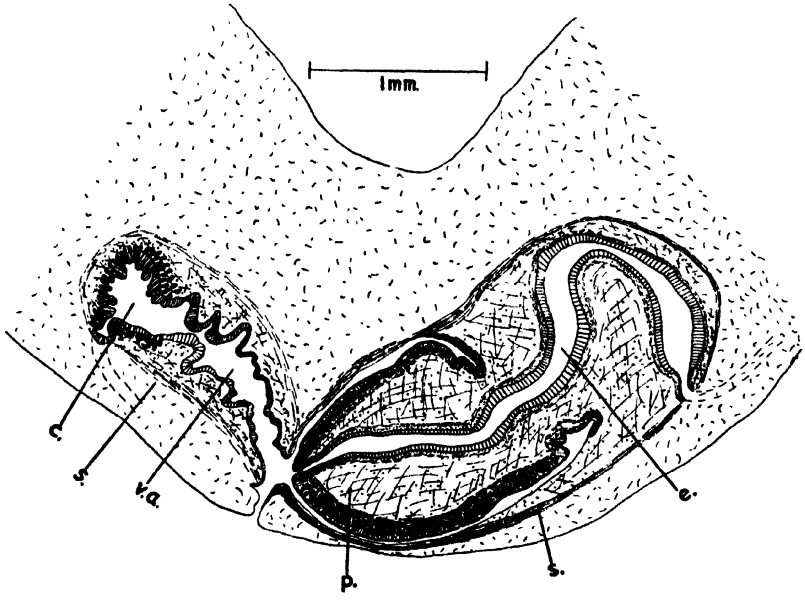

FIG. 8.—*Geodesmus haitiensis*. Sagittal section of copulatory complex (camera-lucida outlines). c., ' shell '-chamber ; e., ejaculatory duct ; p., penis-papilla ; s., muscular sheath ; va., vagina.

GEODESMUS COCKERELLI (Graff, 1899). (Fig. 9.)

Syn. : *Amblyplana cockerelli* Graff, 1899.

This species was originally described on the basis of two specimens collected in Jamaica, and only details of its external features were given. Dr. H. A. Baylis has kindly permitted the writer to cut serial sections from one of the two type-specimens in the British Museum (Natural History), so that the systematic position of the species, according to the classification of the Rhynchodemidae adopted by recent authors, might be ascertained.

The original coloration and markings of the type-specimens have faded considerably, but under moderate magnification and a strong light they may be seen rather faintly to agree with von Graff's description, of which the following is a translation :

' Up to 17 mm. in length and 2 mm. in maximum width. Hinder end conically pointed, anterior end tapering ; both are sharply marked off from the rest of the body by their coloration. The anterior tip is reddish, and behind this, as at the posterior end, lies a wide circular band of yellow. These bands are united by a median dorsal stripe of similar colour. The remainder of the dorsal surface is deep bluish-black, and this colouring extends over the ventral surface for a distance of one-third of the body width on each side. The ' creeping sole ' is yellowish. The mouth is situated at 11 mm. from the anterior end of the body and the genital opening 1·5 mm. behind the

mouth. The two small eyes lie between the reddish tip and the yellow band at the anterior end.'

To this description may now be added the following features, based on the sectioned portion of one specimen :

The body is slightly flattened dorso-ventrally, so that it appears oval in cross-section. Its subepidermal musculature is typical of the Geodesminae Hyman. The subepidermal longitudinal layer is thin, and its fibres are not arranged in bundles. In the parenchyme, forming a sheath investing the digestive and reproductive organs, lies a well-developed longitudinal layer, the fibres of which are collected into bundles.

The copulatory complex is rather small, measuring about 0·75 mm. in length and about 0·5 mm. in maximum width. Only the male copulatory apparatus appears to be invested with a thick muscular sheath, which lies somewhat obliquely, its anterior end being tilted towards the dorsal side.

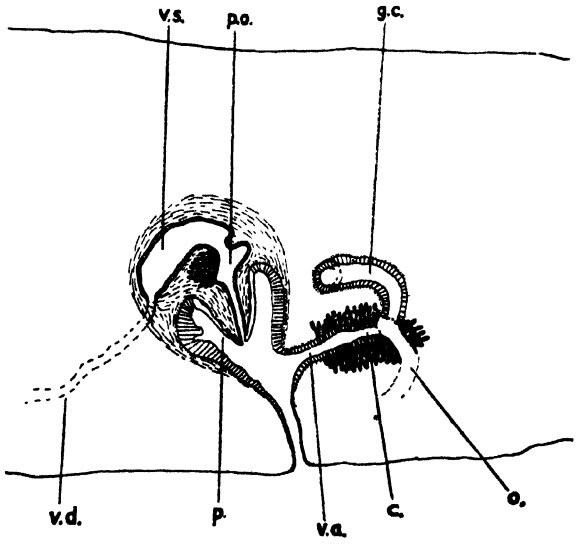

FIG. 9.—*Geodesmus cockerelli*. Sagittal section of copulatory complex (camera-lucida outlines). *c.*, ' shell '-chamber ; *g.c.*, genito-intestinal canal ; *o.*, oviduct ; *p.*, penis-papilla ; *p.o.*, prostatic organ ; *va.*, vagina ; *v.d.*, vas deferens ; *v.s.*, seminal vesicle.

The numerous testes are arranged in two irregular rows, situated ventrally to the gut-branches. The vasa deferentia lie ventrally to the testes and open separately into a relatively wide seminal vesicle. The posterior end of the latter turns ventrally to open into a somewhat smaller vesicle, round the ventral half of which lie numerous extracapsular gland-cells opening into its lumen. The latter vesicle probably represents a prostatic organ, from which a short ejaculatory duct extends to the apex of a moderately-developed penis-papilla. The ejaculatory duct and its modifications—the seminal vesicle and prostatic organ—are lined with a ciliated epithelium.

The oviducts lie ventrally to the gut-branches and laterally to the vasa deferentia. They open separately into the hinder end of a ' shell '-chamber, which is situated at the posterior end of the relatively short vagina. Around the ' shell '-chamber and the hinder portions of the oviducts lie numerous gland-cells which open into the lumen of each. The hinder end of the ' shell '-chamber opens, above the openings of the oviducts, into a genito-intestinal canal which runs anteriorly as far as the muscular sheath of the male apparatus, where it turns sharply towards the left side of the body

to enter the main-gut on that side. The female copulatory apparatus is lined throughout with a ciliated epithelium and coated with a moderately-developed musculature, principally of circular fibres.

This species appears to be easily separated from other species of *Geodesmus*, *sensu* Hyman, recorded from the American continents by the colour-pattern of the body and by the possession of a genito-intestinal canal. The latter character occurs in several species of *Geodesmus* recorded from other parts of the world, and is not regarded as of generic importance.

In conclusion, the writer would like to take this opportunity of thanking Dr. H. A. Baylis for advice given during the preparation of this report.

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On the Polychaeta collected by Mr. J. Colman at St. Helena.

By J. H. Day, Ph.D., Professor of Zoology, University of Capetown.

(With 4 Text-figures.)

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I. INTRODUCTION AND ECOLOGY.

This account is based on a collection of Polychaet worms obtained by Mr. Colman from St. Helena in 1945. A general account of the marine biology of the island has been given by him (Colman, 1946) from which the following data have been extracted. The island lies in the tropical south Atlantic, nearly 16 degrees south of the equator ; it is 1,080 miles off the coast of tropical west Africa and 700 miles south-east of Ascension Island, which is the nearest land. The whole of the island is volcanic, with precipitous shores and a steep narrow submarine shelf ; there are no coral reefs. The sea temperature ranges from 21 to 25 degrees Centigrade ; the maximum tidal range is about one metre, there is very heavy surf on the south-eastern coasts due to the prevailing south-east trade winds, but the seas on the north-western shores are usually more moderate.

The Polychaet collection consists of over 500 specimens collected on the shore between the tide-marks and dredged from depths down to 40 fathoms. Thirty species are included as well as the tubes of three others. These are listed below :—

Species.	Distribution.
Harmonthoe sanctae-helenae, sp. nov.	
Pholoë dorsipapillata Marenz.	Azores, Mediterranean.
Eurythoe complanata (Pallas).	Circumtropical.
Hermodice carunculata (Pallas), var. *didymobranchiata*, Baird.	Ascension, tropical West Africa.
Phyllodoce mucosa Oersted.	North Atlantic.
Phyllodoce macrophthalma (Schmarda).	Madeira, North Atlantic.
Phyllodoce colmani, sp. nov.	
Syllis prolifera Krohn.	Atlantic and Mediterranean.
Syllis variegata Grube.	Universal in tropical and temperate waters
Syllis gracilis Grube.	Circummundan.
Syllis elongata, sp. nov.	
Syllis sp. ?	
Eusyllis sp. ?	
Opisthosyllis brunnea Langerhans.	West Africa, Madeira, West Indies.
Odontosyllis polycera (Schmarda).	West Africa and generally through the sub-tropics of the southern hemisphere.
Pionosyllis longicirrata Saint-Joseph.	Atlantic and Mediterranean.
Exogone verugera (Claparède).	Madeira, Mediterranean, Australia.
Exogone heterosetosa McIntosh.	South Atlantic, Cape, West Africa.
Autolytus pictus (Ehlers).	Atlantic and Mediterranean.
Myrianida pinnigera (Montagu).	North Atlantic and Mediterranean.
Nereis nanciae, sp. nov.	
Glycera lapidum Quatrefages.	Atlantic.
Staurocephalus rubrovittatus Grube.	Atlantic and Mediterranean.
Eunice gracilis (Crossland).	Indo-pacific.
Lumbriconereis coccinea Renieri.	Atlantic and Mediterranean.
Polyophthalmus pictus (Dujardin).	Atlantic, Indian, Pacific.
Armandia intermedia, Fauvel.	Tropical West Africa.
Dasybranchus caducus Grube.	Atlantic, Indian, Pacific.
Pronospio malmgreni Claparède.	North Atlantic and Mediterranean.
Audouinia punctata (Grube).	Tropical Atlantic and Indian Ocean.
Sabellariid tubes, g. et sp. ?	
Branchiomma vesiculosum (Montagu) ?	Atlantic, Mediterranean, Indian Ocean.
Serpula vermicularis Linn.	Atlantic, Mediterranean, Red Sea.
Spirorbis sp. (tubes only).	

The above list of species with their distribution shows that four or possibly six species are endemic, and an equal number are universal in tropical or temperate waters. The rest are Atlantic or Atlantic-Mediterranean species, many of which have been recorded from Madeira or the Azores and some from the West Indies ; only two, *Odontosyllis polycera* and *Armandia intermedia*, might be described as Tropical West African ; only one of the six species recorded by Monro, 1930, from Ascension is present in this collection, and there are no South African species or any evidence of an Antarctic element. Colman states that 'To judge from the three groups which have been at all well studied (molluscs, echinoderms and fish), about a quarter or a third of the St. Helenian species are peculiar to the island ; the closest relationships of the fauna are with that of the West Indies and the next closest with those of the Mediterranean and West Africa ; there are only slender links with South Africa.' The distribution of the Polychaeta fits in very well with this statement, though there is a smaller proportion of endemics and a greater affinity with the fauna of the Azores and Madeira than with that of the West Indies. The comparison of these thirty species with six from Ascension does not permit of any real conclusions, but the absence of a South African component is significant. Work on the planktonic Copepoda of the South African seas at present being prepared for the press by Mr. R. R. Charter of this University, indicates that the cold Benguela current which sweeps along the west coast of South Africa keeps close inshore until it reaches the border of Angola, where it becomes considerably warmer and where all the characteristically South African species disappear. It is thus probable that South African forms never extend anywhere near St. Helena, which is bathed by the central part of the South Atlantic gyral. If this is so, the presence of drifting kelp must be due to wind action alone.

The most striking thing about the whole Polychaet collection is the tiny size of almost every specimen. Not only are the families which include the smallest worms the best represented, but species which are large elsewhere are dwarfed in St. Helena. For example, the family Syllidae, which includes some of the smallest Polychaets, is represented in St. Helena by 13 out of 30 species, and the St. Helenian Syllids are less than half the size of those found elsewhere.

Again, the Amphinomid *Eurythoe complanata* which normally reaches a length of 60 to 100 mm., is 15 to 30 at St. Helena, and the only St. Helenian Nereid, *Nereis nancae*, averages 20 mm. as compared with 40 to 80 mm. of most Nereids elsewhere. There are only two exceptions to this rule : one is *Hermodice carunculata*, which is commonly found on wreckage drifting on the high seas, and the other is the unknown Sabellariid whose empty tubes have a bore of 10 mm. which is rather larger than the average for the family.

II. SYSTEMATIC ACCOUNT.

Family APHRODITIDAE.

Harmothoe sanctae-helenae, sp. nov. (Type St. H. 10 *b*.)

Records.—Three specimens from the sponge *Chondria plebia* dredged in 20 to 25 fathoms off Jamestown, 30/6/45. Eight specimens from algal felt in a rock pool at Banks, 14/6/45. Five specimens dredged off Jamestown in 40 fathoms, 27/6/45. One specimen dredged off Ladder Hill in 10 fathoms, 25/6/45. Two specimens dredged in Prosperous Bay in 15 fathoms, 11/6/45. Six specimens dredged off Banks Point in 10 fathoms, 5/6/45.

Diagnosis.—Very similar to *H. longisetis* ; head with well-marked frontal horns ; elytra deciduous, smooth, pale, with minute capstan-shaped tubercles, no fringes ; dorsal bristles minutely bifid at the tip, ventral bristles slender with fine bifid tips.

Description.—The largest example is only 11 mm. long with 35 segments ; the breadth including the bristles is 3 mm. and the body without parapodia is 1 mm. wide. The colour in spirit is pale yellowish brown with darker pigment on the anterior part of the prostomium and with transverse bands across the back of each of the anterior segments (see fig. 1 *a*). The extent of this pigmentation is very variable ; it may be

completely absent or present along the whole length of the body with extensions on to the base of the cirrophores. The antennae and dorsal cirri are slightly darker than the general colour of the body. The elytra are usually absent, but when present they are yellowish brown with a diffuse patch of dark pigment towards the external margin.

The head (fig. 1 *b*) is as broad as long with prominent brown peaks and two pairs of eyes of which the anterior are the larger and on the extreme lateral margins of the head. The median tentacle is sparsely ciliated and tapers evenly to a filiform tip, the whole tentacle being twice the length of the prostomium. The lateral tentacles are ventral in origin, taper like the median and are roughly equal in length to the postomium. The parapodia are long and pointed so that parapodium plus bristles equals the width of the body proper. Elytra scars are present on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 26, 29, 31 ; the elytra themselves (fig. 1 *d*) are soft, fragile, and very deciduous. They are almost round, apparently smooth but actually covered with minute capstan-shaped tubercles (fig. 1 *e*), and with a few soft finger-shaped papillae. The basal half of the dorsal cirrus is pigmented. In some worms the dorsal cirri increase in length posteriorly until they are markedly longer than the ventral bristles. The ventral cirri are always slender, unpigmented and without claviform papillae. The dorsal bristles (fig. 1 *f*) are stout and increase in length inferiorly. The superior ones have short simple tips, but the longer inferior ones have longer tips which are minutely bifid. The ventral bristles (fig. 1 *g*) are long and slender and spinulose for a considerable extent, particularly the superior ones. All have bifid tips, the superior ones minutely bifid, but the majority have the second tooth one-third the length of the apical one and diverging from it.

I believe this species to be allied both to *H. longisetis* and to *H. spinifera*. As far as I know the former species has not been recorded from the southern hemisphere. Judging by the description given in Fauvel, 1927, p. 66, fig. 24 *a–g*, it has obtuse frontal peaks, eyes partly hidden, minute horny papillae on the elytra, conical dorsal rami to the parapodia, short dorsal bristles with short conical tips and ' parfois un petit sillon longitudinal.' Fig. 24 *d* shows a blunt tip. The ventral bristles differ from the St. Helenian material in having large spinules and a long, fine, secondary tooth in line with the shaft ; moreover, the inferior ones are occasionally unidentate. I have also compared the St. Helena material with South African examples of *H. waahli* (Kinberg), the southern representative of *H. spinifera*, but in this case the deep split in the tips of the dorsal bristles and the large secondary tooth and short spinulose portion of the ventral bristles allows of no confusion.

Distribution.—St. Helena.

Pholoë dorsipapillata Marenz.

Fauvel, 1923, p. 119, fig. 44 *n–q*.

Records.—One specimen from the sponge *Chondria plebia* dredged in 20–25 fathoms off Jamestown, 30/6/45. Two specimens dredged off Jamestown in 40 fathoms, 27/6/45.

Notes.—Typical.

Distribution.—Azores and Mediterranean.

Family Amphiomidae.

Eurythoe complanata (Pallas).

E. alcyonia Gravier, 1901, p. 248, text-figs. 257–268, pl. 9, figs. 140–143, pl. 10, figs. 144–146.

Records.—Numerous specimens from algal felt in a rock pool at Banks.

Notes.—The bristles of this species are not only very variable but are also very easily damaged by preservatives. In the present specimens the anterior dorsal bristles are distinctly bifid, but in the middle and posterior parts of the body the longer arm becomes very long and hair-like while the shorter arm is reduced to a spur and then to a minute knob or step. Harpoon bristles also appear in these posterior

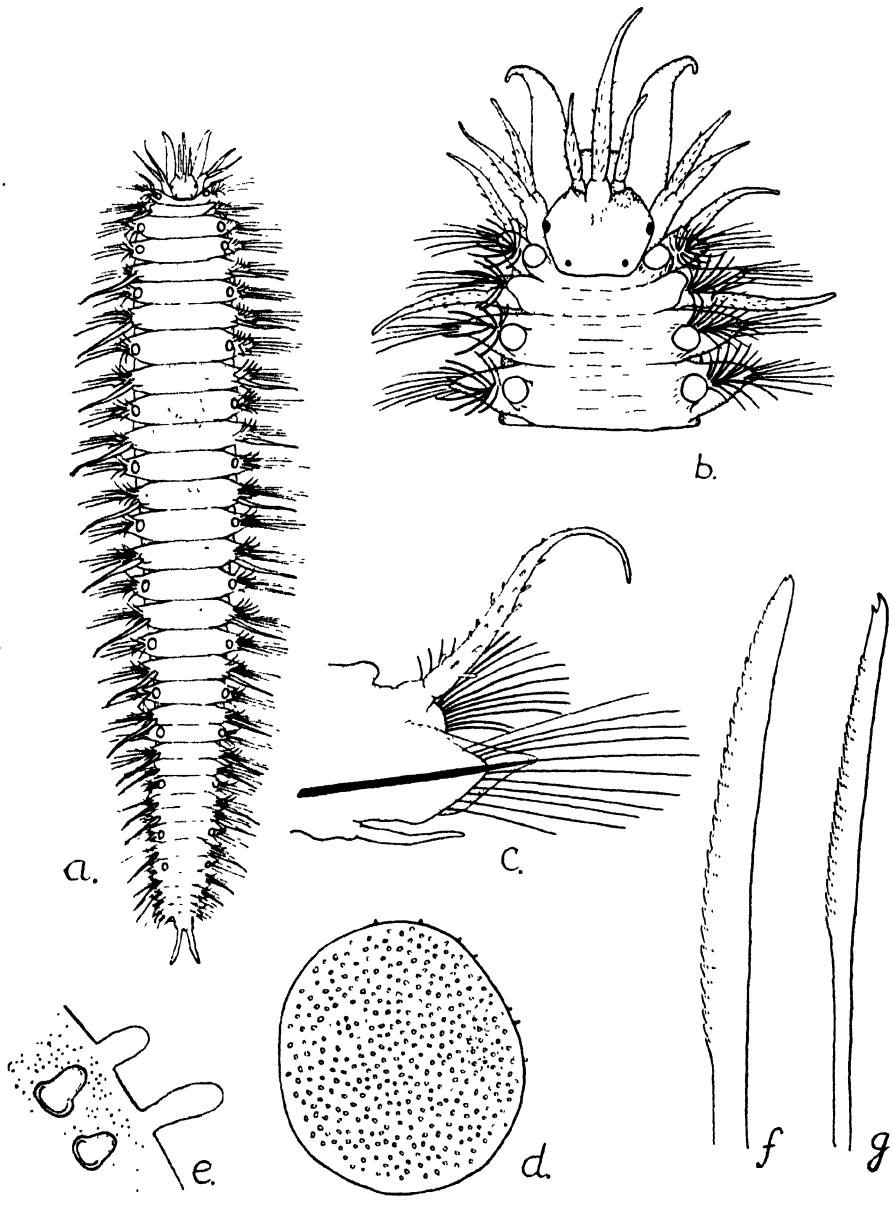

FIG. 1.—*Harmothoe sanctae-helenae*, sp. n.

a, entire worm ; *b*, head ; *c*, parapodium ; *d*, elytron ; *e*, tubercles and papillae ; *f*, dorsal bristle ; *g*, ventral bristle.

segments. The ventral bristles are all strongly forked with a few coarse serrations on the inner side of the longer arm. The specimens are all less than 20 mm. in length, the same size as those from Ascension Island described by Monro, 1930.

Distribution.—Circumtropical.

Hermodice carunculata (Pallas) var. **didymobranchiata** (Baird).

Fauvel, 1914, pp. 113–116, pl. viii, figs. 22–27, 31–32.
Monro, 1930, p. 27.

Records.—Six specimens found in a lobster pot in 8 fathoms close to the cliffs at Horsepasture Point.

Notes.—Typical except that the serrations of the dorsal harpoon bristles have largely disappeared in the preservative.

Distribution.—Tropical West Africa, Ascension Island, St. Helena.

Family PHYLLODOCIDAE.

Phyllodoce macrophthalma Schmarda.

Fauvel, 1923, p. 146, fig. 51 *f–g*.

Records.—One specimen from the sponge *Chondria plebia* dredged off Jamestown in 20–25 fathoms, 30/6/45.

Notes.—According to Fauvel this species may be a juvenile *P. laminosa*.

Distribution.—Atlantic.

Phyllodoce colmani, sp. nov. Type St. H. 14 *b*.

Records.—One specimen dredged off Jamestown in 40 fathoms, 27/6/45.

Diagnosis.—Prostomium ovoid to cordiform, eyes large, no sign of an occipital button. Body markedly elongated, dorsal cirri broadly lanceolate, ventral cirri pointed, twice as long as setigerous lobe. Broad intersegmental bars of black pigment between all body segments.

Description.—It is with some hestitation that I describe this as a new species, since the single specimen had its pharynx retracted and dissection did not reveal clearly what it was like. It is a markedly slender and elongated worm with a length of 38 mm. and a breadth of 1 mm. and about 160 segments. The general colour is transparent white with broad intersegmental bars of black across the dorsum and patches on the dorsal cirrophores (fig. 2 *b*). The head (fig. 1 *a*) is ovoid to cordiform with four swollen antennae and two large black eyes. There is no sign of an occipital button. The tentacular cirri are four in number according to the formula $1+\frac{1}{1}+S\frac{1}{N}$. The first segment is not visible from below, the second segment is without bristles, has a long dorsal and a slightly compressed ventral cirrus, and the third segment has a long dorsal cirrus, a small bristle-bundle and a normal ventral cirrus similar to those of the body segments.

The retracted pharynx extended back to the ninth setiger. All that can be said for certain about it is that the distal portion connected to the intestine is ridged, while the shorter, oral end is papillose. The parapodia (fig. 2 *c*), have oval, lanceolate dorsal cirri, which increase in length posteriorly. The setae arise from a bilobed process of which the anterior lobe is slightly longer. The ventral cirri are attached only at the base of the setigerous lobe, are pointed and double the length of the setigerous lobe. The bristles (fig. 2 *d*) are normal, heterogomph spinigers ; the shafts are straight and the swollen tips are minutely spinulose. The apices, which are slightly recurved, are attached by narrow necks and expand to form blades equal in width to the heads of the shafts and then taper evenly to long fine tips.

Distribution.—St. Helena.

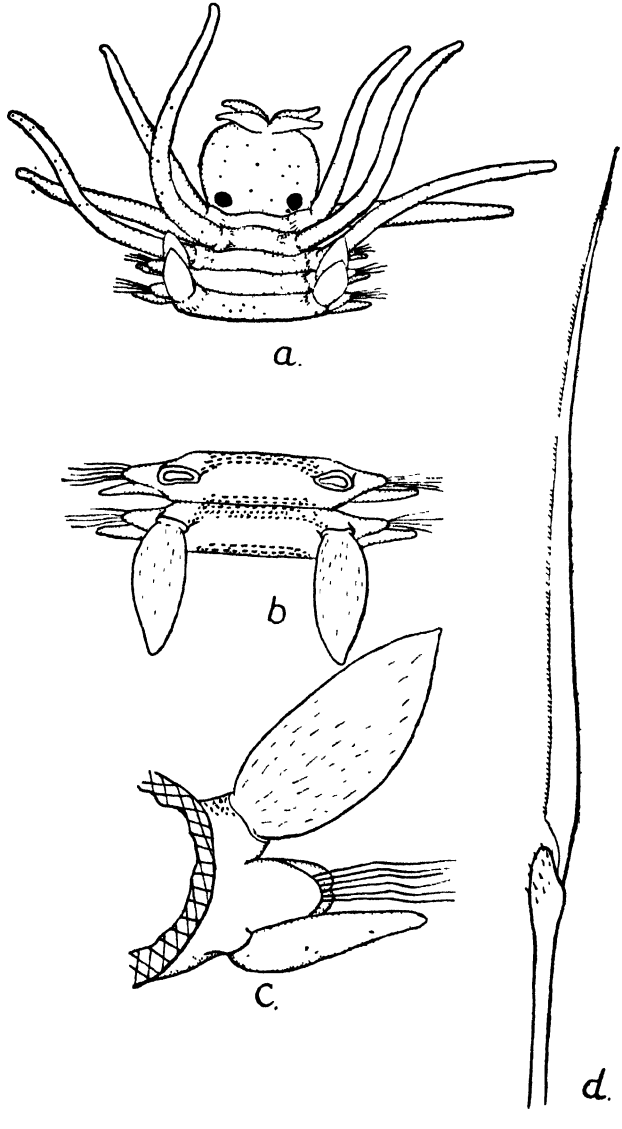

FIG. 2.—*Phyllodoce colmani*, sp. n.
a, head ; *b*, middle segments showing pigmentation ; *c*, parapodium ; *d*, bristle.

Phyllodoce mucosa Oersted.

Fauvel, 1923, p. 152, fig. 154 *a–e*.

Records.—Two specimens from the sponge *Chondria plebia* dredged off Jamestown in 20–25 fathoms, 30/6/45. One specimen dredged off Jamestown in 40 fathoms.

Notes.—Bristles on third segment doubtful ; very close to *P. madeirensis*.

Distribution.—North Atlantic, Adriatic ?, St. Helena.

Family Syllidae.

Syllis prolifera Krohn.

Fauvel, 1923, p. 261, fig. 97 *a–g*.

Records.—Four specimens from the middle third of the intertidal zone among algae, West Rocks, Jamestown Bay, 28/5/45. One specimen from low water mark among algae, Jamestown Steps, 30/5/45. Two specimens from a boat's bottom (two months water), Jamestown Bay, 23/6/45.

Notes.—From the records it would appear that this species can reach adult size in two months. The bristles are long, with bidentate apices and a simple acicular bristle occurs in the last few segments. The dorsal cirri have about 25 articulations. The pharynx is short. One of the specimens collected 30/5/45 is developing a sexual bud.

Distribution.—Atlantic, Mediterranean.

Syllis variegata Grube.

Fauvel, 1923, p. 262, fig. 97 *h–n*.

Records.—Two specimens from the lowest third of the intertidal zone among algae, West Rocks, Jamestown Bay, 28/5/45. One specimen from the Mooring Buoy, Jamestown (12 months in water), 4/7/45.

Notes.—The two species *S. prolifera* and *S. variegata* are very closely related, the main distinguishing features being a longer pharynx, a more anterior tooth and longer dorsal cirri in *S. variegata*. Possibly the one is no more than a variety of the other. The specimens from the West Rocks, Jamestown Bay and from the Mooring Buoy are curious in having sinuous pharynx but are otherwise similar to *S. variegata*. The specimens dredged from the Lighter Moorings have two narrow black bars across each of the anterior segments.

Distribution.—Universal in tropical and temperate waters.

Syllis gracilis Grube.

Fauvel, 1923, p. 259, fig. 96 *f–i*.

Records.—One specimen from dredgings at the Lighter Moorings, 10 fathoms, Jamestown Bay, 23/6/45. One specimen from the sponge *Chondria plebia* dredged in 20–25 fathoms, Jamestown Bay, 30/6/45.

Notes.—Typical.

Distribution.—Circummundan.

Syllis elongata, sp. nov.

Records.—Two specimens from dredgings in 12–20 fathoms off Sugar Loaf Hill, 5/6/45. One specimen from a boat's bottom in Jamestown Bay which had been two months in the water, 23/6/45. One specimen from the lower half of the intertidal zone at the Dockyard, Crown Point, 11/6/45.

Diagnosis.—Long and slender with elongated segments. Dorsal cirri uniformly slender, not tapering, with 15 to 25 articulations. Bristles strongly bidentate, second tooth larger than the apical one. Dorsum and cirri speckled with black.

Description.—These are very slender, elongated worms with the middle segments as long as they are broad. The anterior segments are the same length, but here the

body is swollen by the pharynx and proventriculus. The posterior region is also swollen by sexual products so that the length of the segments is most marked in the middle of the body. The general colour is pale in spirit and transparent in glycerine, but the dorsal cirri and the backs of some of the middle segments are sparsely speckled with black pigment. In a younger individual of 4 mm. this pigmentation is lacking.

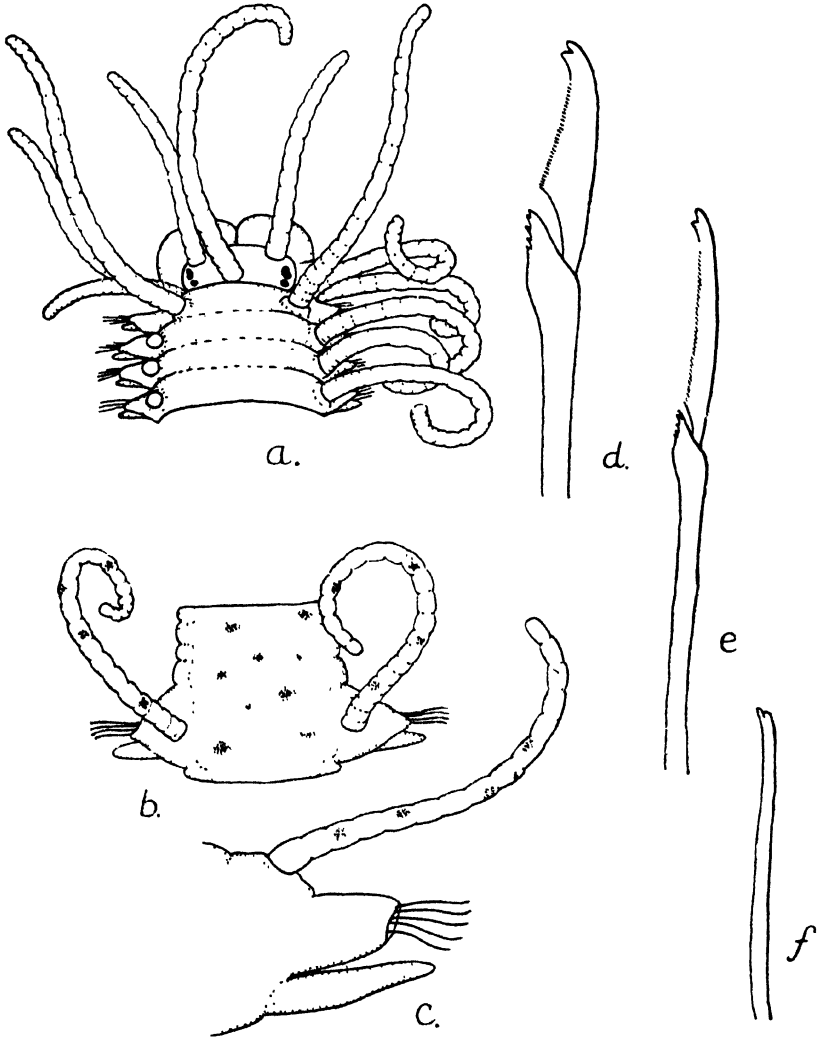

FIG. 3.—*Syllis elongata*, sp. n.
a, head ; *b*, middle segment ; *c*, parapodium ; *d*, normal bristle ; *e*, bristle of third segment ; *f*, posterior simple bristle.

The head (fig. 3 *a*) is broader than long and the palps are bent ventrally but not fused. There are four eye-spots, the median tentacle has about 25 rather indistinct articulations, and the shorter laterals about 15 ; none pigmented. The tentacular cirri are similar to the tentacles. The pharynx is very short, extending only to the fourth setiger

and has a single anterior tooth and is very pale brown in colour. The proventriculus is barrel-shaped, extends to the ninth setiger and there are lateral caeca behind it. The dorsal cirri of the first setiger arise well above the setigerous lobes and even dorsal to the tentacular cirri. The body segments (fig. 3 *b*) are rounded and in the middle of the body they are as long as they are broad, with the parapodia forming blunt conical projections on either side of the posterior half of the segment. The dorsal cirri (fig. 3 *c*) arise well above the origin of the setigerous lobes ; their length is equal to the width of the body, they are slender and untapered and have about 15 to 25 rather indistinct articulations often speckled with black. In the larger individuals they are often coiled like pigs' tails. The ventral cirri are cylindrical and longer than the conical setigerous lobes, which have bundles of 10–12 compound bristles. The bristle shafts have slightly swollen ends and bidentate blades with the second tooth slightly longer than the apical one (fig. 3 *d*). There are also two acicula with obliquely truncate tips in each parapodium. The bristles do not vary greatly in length along the body ; in the anterior segments all the bristles have longer and finer blades (fig. 3 *e*), but within a single bundle there is not the sharp distinction into long and short blades which characterizes the subgenus *Ehlersia*. In the posterior segments the ends of the bristle-shafts are broadened and serrated along the longer margin, and one or two fine simple bristles may occasionally be seen (fig. 3 *f*).

Distribution.—St. Helena.

Syllis ?

Records.—One specimen from the lower half of the intertidal zone at the Dockyard, Crown Point, 11/6/45.

Notes.—The head, pharynx, and bidentate bristles are similar to those of *S. variegata*, but in the middle region of the body the short dorsal cirri of alternate segments are swollen to an oval shape. I have found no account in the literature which fits this peculiar form, but hesitate to describe it as a new species on the basis of a single small specimen.

Distribution.—St. Helena.

Ophisthosyllis brunnea Langerhans.

Langerhans, 1879, p. 541, fig. 7.
Augener, 1918, p. 274, text-fig. xxv.
O. nuchalis Verril, Monro, 1933, p. 255, text-fig. 7.

Records.—One specimen from the upper half of the intertidal zone at the Dockyard, Crown Point, 11/6/45. One specimen from a boat's bottom which had been two months in the water, 23/6/45. One specimen from the lower half of the intertidal zone at the Dockyard, Crown Point, 11/6/45.

Notes.—I have been unable to obtain copies of either Langerhans' or Verril's original papers, but these specimens from St. Helena agree with the descriptions of both Monro and Augener except in regard to coloration and length of pharynx. The head, dorsal cirri and bristles are identical in both descriptions, but whereas Augener describes the surface colour as pale rust yellow to rust brown, Monro's specimens were colourless except for the brown pharynx. The specimens from St. Helena are pale brown on the dorsal surface of the anterior segments, but in the posterior part of the body the pigment is concentrated into an intersegmental spot, and the pharynx is very pale. In Augener's specimens from West Africa the pharynx extends to the 11th and the proventriculus to the 17th setiger ; in Monro's specimens from Florida the comparable figures are 9 and 18, while in this material from St. Helena the figures are 15 and 24. However, since the proportions are roughly similar, I do not feel that the exact number of segments merits specific distinction, and agree with Monro that Verril's species is no more than a colourless form of *O. brunnea*, which thus has a wide distribution over the tropical and subtropical Atlantic including the Annobon Islands, Madeira, Bermuda, Florida, the West Indies and St. Helena.

Odontosyllis polycera (Schmarda).

Augener, 1918, p. 283, pl. v, fig. 97.
Monro, 1933 *a*, p. 36, text-fig. 15.

Records.—One specimen from the sponge *Chondria plebia* dredged in 20–25 fathoms off Jamestown, 30/6/45.

Notes.—The single specimen was only 5 mm. long and probably immature. It is completely colourless. However, the armature of the pharynx, the 40 rows of points on the proventriculus, the shape of the parapodia and the setae with swollen ends to the shafts and strongly bidentate blades agree perfectly with Monro's figures. On the other hand, the antennae are slightly longer and thicker and the dorsal cirri occasionally show evidence of articulations. Augener, 1918, describes the second tooth of the bristles as being half-way along the blades; in the St, Helenian material this second tooth is nearer the tip but still well separated from it, as shown by Monro's figure 15 *f*. *O. polycera* is closely related to *O. fulgurans* Claparède, differing in the size of the tentacles and the eyes; the occipital gibbosity is also larger and pigmented in *O. polycera*. The specimen from St. Helena is somewhat intermediate in these respects.

Distribution.—Panama and the subtropics of the southern hemisphere including New Zealand, Australia, South Africa, St. Helena.

Eusillis, sp.

Records.—Two specimens dredged off Jamestown in 40 fathoms, 27/6/45.

Notes.—Both are anterior fragments, the larger 4 mm. in length with a breadth of 0·3 mm. and the smaller 3 mm. with a breadth of 0·4 mm. They are colourless except for incomplete transverse brown bars across the dorsal surfaces of the anterior segments; these markings consist of short streaks extending from the bases of the dorsal cirri towards the centre and a wider bar across the posterior margin of each segment which may be represented as ‾ _ ‾. The prostomium is oval and broader than long, there are four eyes set in a rectangle with the posterior pair half the size of the anterior. The antennae are not articulated, the median being double the length of the laterals, which are equal to, or slightly longer than the breadth of the prostomium. The palps are united only at the base. The body is rounded in section and the anterior region is slightly tapered. The dorsal cirri which are not articulated are slightly swollen at the base and then taper markedly towards the tip. The dorsal cirri of the first segments are equal in length to the width of the body, but later ones decrease to two-thirds the body width or about twice the length of the parapodia. The ventral cirri are broadly conical and slightly shorter than the setigerous lobes. Each bristle bundle contains about 15 compound, unidentate bristles, two or three of the superior ones having very long narrow blades. The pharynx, which extends to the fifth setiger, has a single anterior tooth and a doubtfully denticulate edge; the proventriculus extends from the 6th to the 12th setiger and has about 50 rows of points.

I know of no species which fits this description; there are many similarities with *E. assimilis* Marenzeller, but the bristles of the latter are bidentate, whereas the *S. Helenian* specimens have obviously unidentate ones. I am, however, very dubious about creating a new species on the basis of two fragmentary specimens.

Pionosyllis longicirrata Saint Joseph.

Fauvel, 1923, p. 288, fig. 110 *h–l*.

Records.—One specimen from algal felt in a rock pool at Banks, 14/6/45. Two specimens dredged off Jamestown in 40 fathoms, 27/6/45.

Notes.—Typical except that the palps are almost separate.

Distribution.—Atlantic, Mediterranean.

Exogone verugera (Claparède).

Fauvel, 1923, p. 307, fig. 117 *m–r*.

Records.—Two specimens dredged off Sugar Loaf Hill in 12–20 fathoms, 5/6/45.

Notes.—One specimen is a female carrying developing young attached to her parapodia by their posterior ends. The tentacles are difficult to see but appear to be short and all of equal length. There are small dorsal cirri on all segments and the ventral cirri are slightly shorter than the setigerous lobes. Most of the bristles have short unidentate blades which are often absent, but each bristle bundle also contains a single compound bristle with a long bayonet-shaped blade and a simple bristle with an obliquely truncate tip.

Distribution.—Madeira, Mediterranean, Australia.

Exogone heterosetosa McIntosh.

E. clavator Ehlers, 1913, p. 485, pl. 33, figs. 1–6.
E. heterochaeta Augener, 1918, p. 297 (with synonymy).

Records.—Six specimens dredged off Banks Point in 10 fathoms, 5/6/45.

Notes.—These 6 specimens are very similar to *E. verugera* recorded above, but the median club-shaped tentacle is longer than the prostomium and the laterals are rudimentary. The prostomium itself is twice as broad as it is long, and the palps are fused throughout their length though a median groove remains visible. There are two pairs of eyes, which are sometimes coalescent, and a single pair of ovoid tentacular cirri. The pharynx, which has a single large anterior tooth, extends to the 4th setiger and the proventriculus extends on to the 9th setiger with 20 rows of points. The parapodia are very similar throughout; on all segments including the second there is an ovoid dorsal cirrus shorter than the setigerous lobe and all the conical ventral cirri are of equal length. Each bristle bundle contains three sorts of bristles; 3–4 compound bristles with short, probably unidentate blades, one compound bristle with a long sword-like blade and one simple bristle which is stout and obliquely truncate. In the posterior segments all the compound bristles have shafts with swollen heads. This species, which was first described rather inadequately by McIntosh in the Challenger Reports is, in the opinion of Augener, 1918, the same as that described and beautifully figured by Ehlers, 1913, as *E. clavator* in the Deutches Südpolar Expedition Reports. While I am somewhat doubtful of this synonymy I must accept it as I have not seen the types. The St. Helena material certainly agrees with Ehler's description, but *E. heterosetosa*, *E. hebes* and *E. verugera* are all closely allied.

Distribution.—Subtropical and temperate areas of the southern hemisphere including South America, South-West Australia, South Africa and St. Helena.

Autolytus pictus (Ehlers).

Fauvel, 1923, p. 315, fig. 121 *a–f*.

Records.—One specimen from among algae in the lowest third of the intertidal zone, West Rocks, Jamestown Bay, 28/5/45. Three specimens dredged from 10 fathoms, Lighter Moorings, Jamestown Bay, 28/5/45.

Notes.—The form and setae are typical, but all colour is lacking.

Distribution.—Atlantic, Mediterranean.

Myrianida pinngera (Montagu).

Fauvel, 1923, p. 322, fig. 124 *a–h*.

Records.—One specimen dredged from 10 fathoms, Lighter Moorings, Jamestown Bay, 23/6/45.

Notes.—The colour is uniformly pale, the dorsal cirri are long but not markedly foliaceous, possibly due to shrinkage on fixing.

Distribution.—North Atlantic, Mediterranean.

Family NEREIDAE.

Nereis nanclae, sp. nov. Type St. H. 3 *a*.

Records.—Numerous specimens from practically every collection station from upper part of the intertidal zone at the Dockyard, Crown Point, down to 40 fathoms off Jamestown.

Diagnosis.—All groups of paragnaths present; group VI is a transverse row of 4–6 points; anterior parapodia with five lobes, posterior ones with four and containing a single stout yellow hook formed by the incomplete fusion of shaft and blade.

Description.—These are small nereids with a maximum length of 20 mm. and a breadth of 2·5 mm. The general colour is pale brown with darker markings on the prostomium and with or without a colour pattern on the anterior half of the body. When the coloration is well developed (fig. 4 *a*), there is a dark prostomium with a pale area in the shape of an inverted T extending forward from between the posterior pair of eyes. On each of the anterior segments there are two transverse bars of brown pigment, one along the anterior and one along the posterior margin. Each bar has a gap in the mid-dorsal line, but there is a short bar across the middle of the segment so that the whole may be represented as = – = or a sort of flattened X.

The prostomium is roughly spade-shaped with four well-developed eyes. The peristomium is swollen and has the length of two body segments. The large palpophores are compressed and bent ventrally so that the button-like palpi are almost invisible from above; the finger-shaped antennae reach just beyond the ends of the palpophores. The tenacles are long and rather fragile; the longest extends back to about the 5th or 6th setiger. The jaws are strong, brown, and have five teeth; all groups of paragnaths are present as conical points, which places this species in the subgenus *Neanthes*. Group I consists of two points one behind the other; II is an oblique narrow double row of about 24 small points set close together; III is a scattered oval patch of about 15 points; IV is similar to II but the double row is bent at an angle and the paragnaths at the base of the jaws have transversely elongated bases; V is a single point; VI, which is supported on a prominent pad, consists of a transverse row of four to six points, while VII and VIII form an irregular double row of points of about the same size.

The anterior parapodia (fig. 5 *d*) have five lobes and well-developed dorsal and ventral cirri. The dorsal lobe is slightly longer than the rest. The dorsal bristle-bundle consists of about 12 homogomph spinigers with short tapered blades. The ventral bristles are in two groups, the superior group consisting of about six homogomph spinigers similar to those of the dorsal bundle and two stout heterogomph falcigers; the inferior group consist of a single heterogomph spiniger and about ten heterogomph falcigers (fig. 4 *f*) similar in shape to the superior ones but smaller. The parapodia of the middle segments are very similar to the anterior ones, the main difference being that the dorsal setigerous lobe is reduced and the blades of the superior heterogomph falcigers tend to become soldered on to the shafts. In the posterior parapodia these characters are accentuated. The dorsal setigerous lobe is lost so that the foot is reduced from five lobes to four (fig. 4 *e*). The blade of the single remaining superior heterogomph falciger is firmly fused to the shaft to form a stout yellow hook in which the breakage plane is still visible (fig. 4 *g*). Here, also, the dorsal lobe of the foot becomes expanded and pigmented at the base and has a conical apex. The dorsal cirrus is reduced but is still longer than the dorsal lobe. The dorsal bristle-bundle has now only six homogomph spinigers; the superior ventral group consists of three homogomph spinigers and the yellow hook, while the inferior ventral group is reduced to two heterogomph spinigers and three heterogomph falcigers with guards and short blades (fig. 4 *h*).

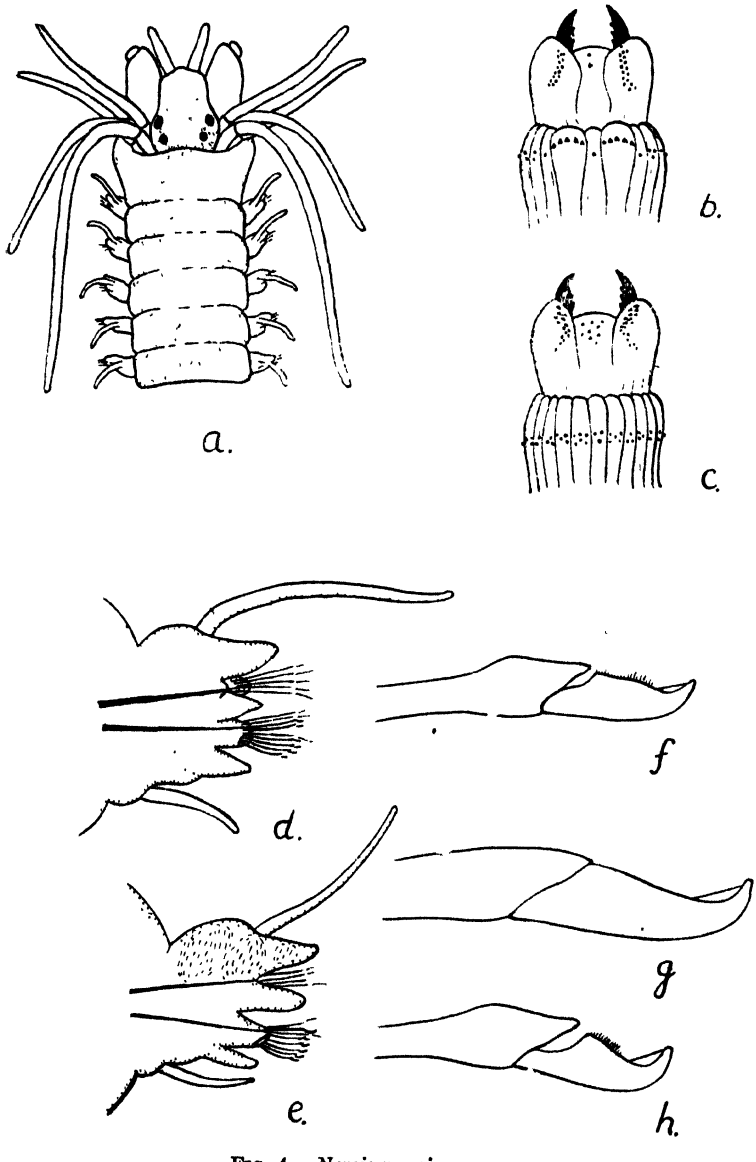

FIG. 4.—*Nereis nanciae*, sp. n.

a, head ; *b*, dorsal view of proboscis ; *c*, ventral view of proboscis ; *d*, anterior parapodium ; *e*, posterior parapodium ; *f*, anterior heterogomph falciger ; *g*, posterior hook ; *h*, normal posterior heterogomph falciger.

Family GLYCERIDAE.

Glycera lapidum Quatrefages.

Fauvel, 1923, fig. 151 *f–m*.

Records.—One specimen from the sponge *Chondria plebia* dredged from 20–25 fathoms off Jamestown, 30/6/45. Four specimens dredged in 10 fathoms off Banks Point, 5/6/45.

Notes.—Papillae on the pharynx typical. The anterior dorsal lobe of the parapodium is so small as to be easily overlooked and the posterior lobe is doubtful; if present, it is rounded and very small. The ventral cirrus is well marked and pointed.

Distribution.—Atlantic, Mediterranean.

Family EUNICIDAE.

Eunice gracilis (Crossland).

Nicidion gracilis Crossland, 1904, p. 327, figs. 65 and 66, pl. 22, figs. 10 and 11.
Fauvel, 1932, p. 140, text-fig. 20 (with synonymy).

Records.—Two specimens from the sponge *Chondria plebia* dredged off Jamestown in 20–25 fathoms, 30/6/45. One specimen from algal felt in a rock pool at Banks, 14/6/45.

Notes.—The material, which consists of two small but complete specimens measuring 9 and 18 mm. and an anterior fragment of 22 mm., was particularly difficult to identify. The two smaller specimens had no tentacular cirri or obvious gills and were at first thought to belong to Ehler's genus *Paramarphysa*, and it is to be noted that Augener has recorded a 7 mm. specimen of *P. longula* from the island of Annobon which is relatively close. On examination, the larger fragment was found to agree with the smaller specimens in every respect except that it possessed a pair of tentacular cirri and thus belonged to the genus *Nicidion*. It seemed reasonable to conclude that tentacular cirri develop at a relatively late stage and that all the specimens were in fact some species of *Nicidion*. Finally, a close examination of the two small specimens revealed the presence of gills as single filaments on the last two segments; these structures were of course missing from the larger fragmentary specimen. The presence of both gills and tentacular cirri placed the material in the common genus *Eunice*, two species of which, *E. siciliensis* and *E. gracilis*, have gills as single filaments in the posterior segments. As shown by Fauvel, 1932, the distinguishing character is the presence of comb setae and articular bristles in *E. gracilis*. The characters of the St. Helena material may now be briefly summarized as follows: palps fused leaving only a small anterior notch, two eyes, five club-shaped, non-articulated tentacles reaching the 2nd setiger, tentacular cirri appearing relatively late. The great dental plates have six sharp teeth and the anterior curved plates about eight; the jaw supports are long and slender. Crossland's large specimens from tropical East Africa had blunt teeth, but this is probably due to age. Dorsal and ventral cirri are present on all parapodia which also have long setigerous lobes reinforced by a projecting aciculum which is yellow in the anterior segments, but becomes black in the posterior ones. The upper bristle-bundle consists of narrow bladed capillaries and comb setae with about ten teeth: the lower bundle consists of a few strongly bidentate falcigers and black, bidentate acicular bristles with guards which appear at about 20th foot. Only in the last two segments of these small individuals were gills found as single filaments.

I have given a full description of these small worms as it is probable that the absence of tentacular cirri and the apparent absence of gills has caused confusion in the past and it is possible that the 7 mm. specimen recorded as *Paramarphysa longula* by Augener from West Africa may be a juvenile *E. gracilis*.

Distribution.—Indopacific, West Africa ?.

Staurocephalus rubrovittatus Grube.

Fauvel, 1923, p. 445, fig. 177 *a–l*.

Records.—One specimen from the sponge *Chondria plebia* dredged in 20–25 fathoms off Jamestown, 30/6/45. One specimen from algal felt in a rock pool at Banks, 14/6/45.

Notes.—Typical.

Distribution.—Atlantic, Mediterranean, Angola.

Lumbriconereis coccinea Renieri.

Fauvel, 1923, p. 432, fig. 172 *g–n*.

Records.—20 specimens from dredgings in 10 fathoms at the Lighter Moorings, Jamestown Bay, 23/6/45. Four specimens from the sponge *Chondria plebia* dredged in 20–25 fathoms off Jamestown, 30/6/45. 11 specimens from algal, felt in a rock pool at Banks, 14/6/45. Two specimens dredged in 10 fathoms off Ladder Hill, 25/6/45. One specimen dredged in 15 fathoms in Prosperous Bay, 11/6/45.

Notes.—This species seems to be common both in the intertidal zone and below. The bristles are typical and there are two teeth on Mx. III, but the prostomium is more oval than spherical.

Distribution.—Atlantic and Mediterranean.

Family Spionidae.

Prinonospio malmgreni Claparède.

Fauvel, 1927, p. 61, fig. 21 *a–e*.
? *P. capensis* McIntosh, 1885, p. 381, pl. 45, fig. 7, pl. 24*a*, figs. 7 and 8.

Records.—Four specimens dredged in 10 fathoms off Ladder Hill, 25/6/45. One specimen dredged in 15 fathoms, Prosperous Bay, 11/6/45. Nine specimens dredged in 10 fathoms off Banks Point, 5/6/45.

Notes.—The characters are typical. On the 10th to 14th setigers, there is a single stout acicular bristle projecting from the bottom of the ventral bristle-bundle ; hooks appear in the ventral ramus of the 14th setiger. Although McIntosh's description of *P. capensis* is incomplete it appears to have the same arrangement of gills and probably refers to this species.

Distribution.—Atlantic, Mediterranean.

Family Cirratulidae.

Audouinia punctata (Grube).

Cirratulus punctatus Augener, 1918, p. 465.; Monro, 1933, p. 264.

Records.—25 specimens from algal felt in a rock pool at Banks, 14/6/45.

Notes.—Body colour chocolate-brown to yellow flecked with black pigment. Prostomium rounded, gills from the first setiger, tentacles on the 4th to 5th. In the anterior part of the body the gills are nearer the dorsal ramus than the distance which separates the rami, in the mid-region the distances are equal. There are three hooks in the ventral ramus from about the 12th setiger and two in the dorsal ramus from about the 20th. Capillaries occur in both rami of all segments. It is surprising that both Monro and Augener retain this species in the genus *Cirratulus*. In all the specimens which I have seen, both from South Africa and St. Helena, the gills start well in advance of the tentacles which is the distinguishing feature of *Audouinia*.

Distribution.—Tropical Indian Ocean, tropical west coast of Africa, St. Helena.

Family OPHELIIDAE.

Armandia intermedia Fauvel.

Augener, 1918, p. 424.

Records.—One specimen dredged off Ladder Hill in 10 fathoms, 25/6/45. One specimen dredged off Banks Point, 10 fathoms, 5/6/45.

Notes.—There are 29 setigers in all, of which the last four are narrowed and without branchiae. The head is similar to that of *A. polyophthalma*, forming an elongated cone terminating in a digitiform palpode. There are three subcutaneous eyes situated on the dorsal and ventrolateral sides of the brain. The nuchal organs are large and evaginable ; gills start on the 2nd setiger and are present on all succeeding ones except the last four. There are 11 to 12 pairs of eye-spots from the 7th setiger. The bristles are in two bundles, the longer dorsal ones arising from the front of the dorsal cirrus and the shorter, posteroventral ones from a knob-like setigerous lobe. The anal tube has no median ventral cirrus at its base, it is obliquely truncate so that it opens somewhat ventrally, and there is a fringe of 10 to 12 cirriform processes around its margin.

Distribution.—Tropical West Africa.

Polyophthalmus pictus (Dujardin).

Fauvel, 1927, p. 137, fig. 48 *l–n*,

Records.—Two specimens from among algae in the lowest third of the intertidal zone, West Rocks, Jamestown Bay, 28/5/45. One specimen from algal felt in a rock pool at Banks, 14/6/45. Two specimens from algal felt just below mean sea-level, Jamestown Steps, 30/5/45. 14 specimens dredged from 10 fathoms off Banks Point, 5/6/45.

Notes.—Form and coloration typical. Although there is considerable variation in size, all the specimens are smaller than the average.

Distribution.—Atlantic, Mediterranean, Red Sea, Indian Ocean, Pacific Ocean.

Family CAPITELLIDAE.

Dasybranchus caducus Grube.

Fauvel, 1927, p. 148, fig. 52 *a–h*.

Records.—One specimen from algal felt in a rock pool at Banks, 14/6/45.

Notes.—This specimen is doubtfully assigned to *D. caducus* since no gills were seen, but *D. caducus* has retractile gills and agrees in all other respects. The St. Helenian specimen is 50 mm. long, which is rather smaller than the average for this species, but is still considerably larger than most of the Polychaets from the island.

Distribution.—Cosmopolitan.

Family SABELLARIIDAE.

Sabelariid tubes.

Records.—Tube fragments from the dredgings in 12–20 fathoms off Sugar Loaf, 5/6/45, and from 40 fathoms off Jamestown, 27/6/45. Four broken tubes dredged from 15 fathoms, Prosperous Bay, 11/6/45.

Notes.—All the tubes are broken and empty. They are constructed of pebbles of volcanic material and appear to have been attached along their whole length and not in the form of colonial masses. This is what is usually found in the genus *Idanthyrsus* a species which, *I. pennatus* has been recorded by Monro, 1930, from Ascension Island. The bore of the tubes is about 10 mm. indicating that the worms were of normal size and not dwarfs like the rest of the Polychaet fauna of St. Helena.

Family TEREBELLIDAE.

Terebellid tubes.

Records.—Broken tubes were dredged from the following stations : 10 fathoms off Ladder Hill, 12–20 fathoms off Sugar Loaf, 40 fathoms off Jamestown.

Notes.—All the tubes are empty and of normal size ; there is nothing to show to what genus they belonged.

Family SABELLIDAE.

Branchiomma vesiculosum (Montagu) ?.

Fauvel, 1927, p. 315, fig. 109 *a–q*.

Records.—One juvenile specimen dredged off Jamestown in 40 fathoms, 27/6/45.

Notes.—This juvenile specimen is 3 mm. long ; it has spatulate dorsal bristles in the thorax and is either *B. vesiculosum* or possibly *B. quadriocultatum*.

Family SERPULIDAE.

Serpula vermicularis Linnaeus.

Fauvel, 1927, p. 351, fig. 120 *a–q*,

Records.—One live specimen and some empty tubes dredged from 40 fathoms off Jamestown, 27/6/45. Two specimens on the carapace of the crayfish *Scyllarus latus* trawled in 38 fathoms off Jamestown, 19/6/45.

Notes.—The specimens are all small and the tubes are partly curled, circular in cross-section or with only a faint median ridge. The operculum is radially symmetrical and its edge has numerous projections. They have therefore been assigned to the common *S. vermicularis*, and not to the closely related *S. concharum*, whose tube is rectangular in section.

Distribution.—Atlantic, Mediterranean, Red Sea.

Spirorbis sp.

Records.—Empty tubes on shells from the lower half of the intertidal zone, Dockyard, Crown Point, 11/6/45. Empty tubes also found on stones dredged from the following stations : 12–20 fathoms off Sugar Loaf, 5/6/45 ; 40 fathoms off Jamestown, 27/6/45.

Notes.—It was surprising to find so many complete yet empty tubes ; possibly the species is a seasonal one. The tubes were all coiled clockwise from origin to mouth and have two marked ridges along their length.

III. SUMMARY,

The collection of Polychaeta obtained by Mr. Colman from St. Helena is described. There are thirty species and the empty tubes of three more. Four species are new. All the specimens are very small except *Hermodice carunculata*. The Polychaet fauna of St. Helena has affinities with the fauna of warm or tropical North Atlantic and Mediterranean ; it has little connection with the fauna of tropical West Africa and none at all with South Africa.

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The morphology of the chondrocranium of *Gymnarchus niloticus*.

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(Communicated by Professor G. R. DE BEER, M.A., D.Sc., F.R.S., P.L.S.)

(With 19 Text-figures.)

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1. INTRODUCTION.

The only existing work on the chondrocranium of *Gymnarchus* is that of Assheton (1907). This forms part of his paper on the development of various organs of *Gymnarchus niloticus*. He described five stages—5, 8, 9, 11 and 43 days old, but his description is very meagre and does not include any definite information regarding the relations of the nerves, veins and arteries to the various cartilages. Norman (1926) mentioned *Gymnarchus* in his paper where he compares the chondrocranium of various Teleostei, but his information, too, is very scanty and does not add much to existing knowledge. Holmgren (1943) described the orbital capsule, containing the eye and the eye-muscles, of *Gymnarchus*, in connection with other Teleostei. Nothing is known, however, about the development of the bony skull of this fish. The adult skull has been described by a few workers—Erdle (1847), Hyrtl (1856), Ridewood (1904) and Gregory (1933).

The present study is based on the examination of two stages in the collection of the Department of Embryology, University College, London, and is mainly on the 15th day larval stage.

This work was done in that Department under Professor G. R. de Beer, F.R.S. I owe a great debt of gratitude to him for his continuous guidance, help and encouragement, which alone made it possible for me to do this work. I wish to thank Miss E. R. Turlington for her help in the preparation of the drawings from my sketches and reconstructions, Dr. E. Palmer for her assistance in the translation of German texts, and Dr. P. Ford for his friendly help.

2. DESCRIPTION.

The chondrocranium of a 15-day larva of *Gymnarchus* is quite well developed. In some places perichondral ossifications have started. Only in a few areas has the

cartilage been replaced to some extent ; in other places the original boundaries of the cartilage are not affected. Most of the membrane-bones are also ossifying.

(a) *The base of the Chondrocranium.*

The base of the chondrocranium (fig. 2) consists of a broad parachordal plate (*ppl*) fused to the posterior ends of the trabeculae (*tc*), which are themselves quite broad and widely separated by a very large hypophyseal fenestra (*hf*). Anteriorly to this fenestra the two trabeculae are joined into a relatively narrow trabecula communis (*tcom*). No interorbital septum is developed ; the brain extends well over the trabecula communis. The skull of larval *Gymnarchus* is, therefore, platytrabic. On the other hand, the adult skull is tropitrabic and an extensive bony interorbital septum is then present (Hyrtl, 1856 ; Ridewood, 1904). No pro-otic bridge is present, hence there is no demarcation between the hypophyseal fenestra and the basicranial fenestra. The place where the trabeculae fuse with the parachordals is not recognizable and there is no appreciable difference of level between the two in in this region. The hypophyseal fenestra is ventrally completely covered by the parasphenoid bone (figs. 8 to 13, *psb*). The internal carotid arteries do not enter the hypophyseal fenestra directly, but have their separate foramina (*icf*) on each side of the fenestra, separated from it by a stretch of cartilage.

The notochord does not extend for the whole length of the parachordal plate, but ends halfway along it In the greater part of the length of this chordal portion the plate is divided into two separate parachordals, no bridge of cartilage extends, either above or below the notochord, from one parachordal to the other. A short distance behind its anterior end, the notochord during its forward course gradually sinks below the level of the parachordals, which accordingly begin to fuse with one another over the notochord. The anterior tip of the notochord lies ventrally to the fused chordal plate and quite separate from it. The size of the notochord in this region of the head, except in the occipital area, is very insignificant.

The median zones of the separate parachordals and of the fused plate lie for their entire length in the same plane. Their lateral areas at first lie in almost the same plane as the middle zone, but gradually they rise above it obliquely, thus the prechordal portion of the plate on the whole assumes the shape of a very broad and shallow trough (fig. 18), while in the chordal region the upward inclination of the lateral regions of the parachordals becomes more pronounced forming an angle with the flat median area, making the trough deep.

The separate trabeculae are wedge-shaped (fig. 10), but the trabecula communis becomes thicker and has smooth dorsal and ventral surfaces (fig. 7). The trabeculae are at the general level of the parachordal plate ; but the trabecula communis gradually rises up.

(b) *The Occipital Region.*

From the posterior region of the parachordals, behind the auditory capsules, arises a pair of occipital arches, separated by the notochord (fig. 1). Each arch fuses with the hind wall of the auditory capsule (*ac*), leaving a large jugular foramen (*jf*) for the exit of the vagus nerve and the posterior cerebral vein. A partial tectum posterius, confluent anteriorly with the tectum synoticum, covers the anterior one-third part of the occipital arches. Behind the posterior edge of the tectum posterius, and wedged between the free dorsal edges of the occipital arches, is a median superior occipital cartilage (fig. 1). It is compressed laterally and its dorsal part rises above the level of the posterior edge of the tectum posterius.

Three pairs of nerves pass out between the skull and the elements of the first vertebra, which consist of a pair of basiventrals and a pair of basidorsals with their upper ends produced into spinal processes. All the three nerves of each side are mixed nerves since besides the ventral nerve roots they also have well formed dorsal roots and ganglia. The three ganglia are located laterally to the side wall of the occipital

arch, the first two are placed close together and the third one a little distance posteriorly. The dorsal and ventral nerve roots of the three nerves, coming from the central nervous system, pass over the slanting dorsal edge of the occipital arch. Thus, though they may be regarded as morphologically posterior or dorso-posterior to the occipital arch, topographically they are located within the territory of the occipital region. The disposition of these nerves in the stages here studied, therefore, gives no clue to their future relations, namely, whether they will emerge through the future definitive foramen magnum, and will thus occupy a position between the exoccipital bone and the first vertebra, or will get entrapped in the growing occipital side wall, and will thus gain an exit through foramina in the exoccipital bone. Neither is it certain that the elements of the first vertebra of this larval stage will constitute the future first free vertebra of the adult skull.

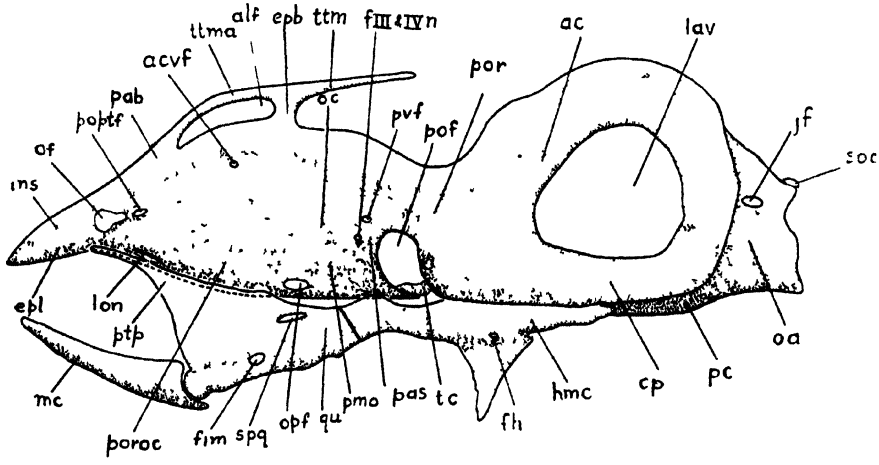

FIG. 1.—*Gymnarchus niloticus.* Graphic reconstruction of the chondrocranium of a 15 day larva, lateral aspect.

(c) *The Auditory Region.*

The auditory capsule is large because the greatly inflated sac-like diverticulum of the air-bladder is included within the auditory cavity of the capsule. The auditory capsule is connected to the basal plate by means of a broad anterior basi-capsular commissure (fig. 2, *abc*) while the posterior connection is established through a comparatively slender and narrow posterior basi-capsular commissure. Between these two commissures, the lateral edge of the basal plate, and the medial margin of the base of the auditory capsule, is a large basi-capsular fenestra (*bcf*). In the width of the anterior commissure there is an area from which cartilage has been secondarily removed. However, this does not create a foramen since the space is occupied by bony lamellae of the pro-otic bone, here developed only in the lower ventral perichondrium of the once present cartilage, which has disappeared together with its upper perichondrium (fig. 17, *pob*).

The glossopharyngeal nerve comes out of the cavity of the auditory capsule immediately behind the posterior edge of the anterior commissure (fig. 2, *gln*). The peculiar position of the exit of this nerve is discussed below.

The head of the hyomandibular cartilage fits in a groove on the ventral surface of the auditory capsule (fig. 16). Procartilage is present in abundance within the groove of the articulation, foreshadowing the future fusion of the hyomandibula with the auditory capsule. A longitudinal ridge of cartilage hangs down ventrally from the base of the capsule, between the posterior half of the hyomandibula and the basi-capsular fenestra (fig. 18, *vrs*). This ridge separates the head vein from the hyomandibular cartilage.

On the lateral wall of the auditory capsule there is a large vacuity (fig. 1, *lav*) in the space between the three semicircular canals. Medially to this vacuity and spreading over its whole expanse is an enormously distended sac-like diverticulum of the air-bladder located within the auditory capsule. The vacuity is completely

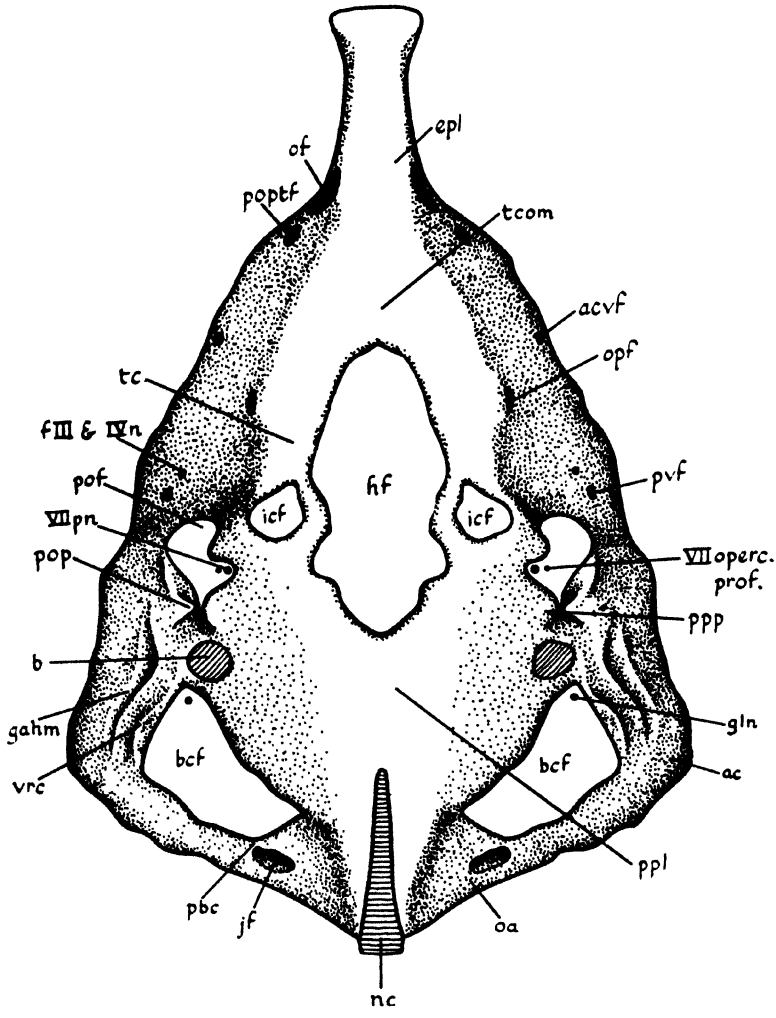

FIG. 2.—*Gymnarchus niloticus*. Graphic reconstruction of the chondrocranium of a 15-day larva, ventral view. (Only that part of the pro-otic bone is shown which fills the space in the cartilage of the anterior basi-capsular commissure).

covered by a delicate membrane. There is, therefore, no direct communication from the auditory cavity to the outside of the skull, neither is the lateral wall of the air-bladder diverticulum 'exposed' in the real sense of the word.

The positions of the anterior and posterior semicircular canals can be traced by the swellings on the external surface of the auditory capsule. Owing to the presence

of the lateral auditory vacuity the cartilage surrounding the horizontal semicircular canal forms a prominent horizontal rim which reflects the position of the canal. This rim is the exaggerated crista parotica of other forms.

Inside the auditory capsule are three cartilaginous septa for the semicircular canals. The shortest of the three is the septum semicirculare anterius (figs. 14, 15, *ssa*), which surrounds for a short distance the foremost portion of the anterior semicircular canal and practically the whole of its ampulla in the region anterior to where the ampulla joins the utriculus. The rest of this canal lies in a broad groove excavated in the thickness of the wall of the capsule (fig. 17). The septum semicirculare laterale (fig. 18, *ssl*) extends along the whole length of the lateral semicircular canal, from a point behind its ampulla to a point in the posterior region of the capsule where the canal turns in the medial direction to join the utriculus. The septum semicirculare posterius is formed underneath the posterior semicircular canal at the point where the canal rises up from the crus commune and comes near the wall of the capsule. This septum extends for almost the whole length of the canal, ending where the canal turns down to join its ampulla. The utriculus and the sacculus are comparatively small and do not come near the wall of the auditory capsule (fig. 18).

The posterior half of the auditory region is roofed over by the tectum synoticum which, as already described, is continuous with the partially developed tectum posterius. A small ledge of cartilage projects latero-ventrally from the outer wall of the auditory capsule in the anterior region of the ampulla of the anterior canal. The dorsal cutaneous trunk of the facial nerve * passes out immediately behind this ledge. The supratemporal branch of the glossopharyngeal nerve after coming out through a foramen in the exoccipital bone turns dorsally and runs through a groove in the posterior aspect of the crista parotica.

(d) *The Orbitotemporal Region.*

An extensively developed orbital cartilage (fig. 1, *oc*) stretching from the auditory capsule to the ethmoid region, and fused with the lateral edges of the trabeculae and trabecula communis, furnishes the complete side wall of the chondrocranium in the orbitotemporal region, save for the foramina for the exit of nerves and blood-vessels.

The various regions of fusion of the orbital cartilage with other elements of the skull may now be considered. Posteriorly it is attached to the auditory capsule by means of a broad postorbital root (*por*), which forms the dorsal and dorso-posterior border of a large foramen—the pro-otic foramen (*pof*). Anteriorly the orbital cartilage is fused with the paraphysial cartilage, and with the lateral edge of the trabecula communis behind the olfactory foramen (*of*). The optic foramen is halfway along the orbital cartilage (*opf*), just above the lateral edge of the trabecula. Thus the ventral border of this foramen is bounded by the trabecula only. The portion of the orbital cartilage between the optic and the olfactory foramina is the pre-optic root (*poroc*). Between the optic and pro-otic foramina the fusion is brought about by the combined pila metoptica and pila antotica secundaria ; the part in front of the oculomotor foramen represents the metoptic root (*mor*), and the portion between the foramen for the pituitary vein (*pvf*) and the pro-otic foramen is equivalent to the pila anotica secundaria (*pas*). The lateral wall extending from underneath the dorsal cutaneous trunk of the facial nerve to the posterior boundary of the pro-otic foramen, and partially covering the trigemino-facialis ganglionic complex, is the forward extension of the auditory capsule, lying anteriorly to the fusion of the septum semicirculare anterius with the wall of the capsule. The ventral border of the pro-otic foramen and the space leading from it latero-ventrally up to the anterior basicapsular commissure is occupied by the pro-otic bone (figs. 13, 14, 15, *pob*). Remains

* This is an extra branch of the facial nerve in *Gymnarchus* and is described in the section dealing with nerves (p. 460).

of the cartilage in the outer side wall of the jugular canal indicate that a complete cartilaginous lateral commissure was present in an earlier stage. This will be referred to again in connection with the trigemino-facialis chamber.

There are no posterior or anterior myodomes. All the eye-muscles are collected into an orbital capsule (figs. 6, 7, *ocp*) whose structure is essentially as described by Holmgren (1943): "The eye-muscles are collected in an orbital capsule, which also encloses the eye. Outside the cornea the capsule merges into the chorium, which is much thickened in that part. The capsule has two conical expansions, of which the shorter, anterior, encloses the obliquus muscles, the longer, posterior, the rectus muscles. The former are inserted into the tip of the anterior cone, the latter in the posterior which extends into a slender tendon, which inserts into the lateral wall of the brain-case below the posterior border of the foramen of the oculomotor nerve", and, "The obliquus group is attached dorsally to the posterior border of the olfactory foramen".

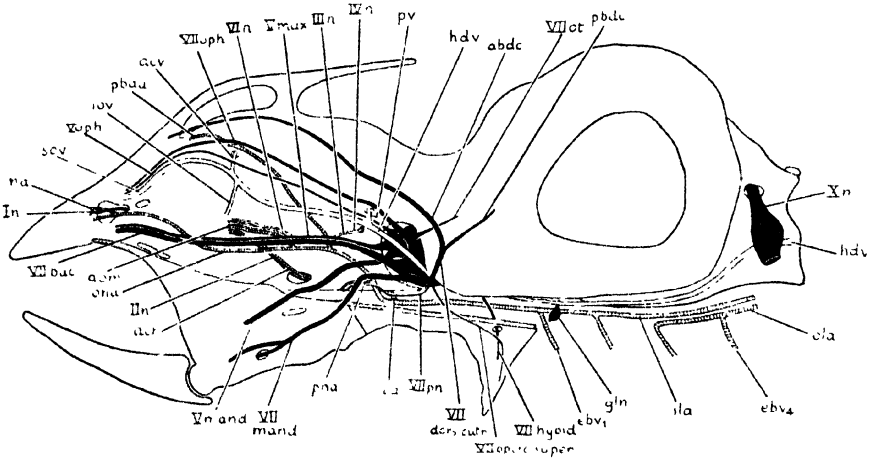

FIG. 3.—*Gymnarchus niloticus*. Graphic reconstruction of the chondrocranium of a 15-day larva, with the chief nerves and blood vessels inserted. The ventral branch of the dorsal cutaneous facialis nerve is omitted for the sake of clarity.

(c) *The Trigemino-facialis Chamber.*

A well developed trigemino-facialis chamber is present, similar in structural details, with minor differences, to the advanced larval stage of *Salmo* (de Beer, 1927). As has already been pointed out, the region from the posterior border of the pro-otic foramen to the anterior basi-capsular commissure is ossified and occupied by the pro-otic bone. The chamber begins behind the dorsal cutaneous trunk of the facial nerve. The extraordinarily enlarged brain and the inclusion of the enormously inflated diverticulum of the air-bladder within the auditory capsule, have brought about a lateral rotation in the position of the auditory capsule, resulting in a displacement of the hyomandibular articulation and of the position of the trigemino-facialis chamber from a latero-ventral position almost to the ventral surface of the skull. The chamber is divided by well developed bony lamellae (fig. 14) into two parts—the pars ganglionaris (*pg*) lodging the trigeminal and facial ganglia and the pars jugularis (*pj*) housing the head vein (*hdv*). Thus these bony lamellae form the lateral wall of the pars ganglionaris and the medial wall of the pars jugularis. The medial wall of the pars ganglionaris is formed by the dura mater, and the lateral wall of the pars jugularis by the outer lamella of the pro-otic bone.

Some details regarding the chamber will be considered now. Just before entering the pars jugularis, the head vein running from front to back comes very close to, and is in actual contact with, the facial ganglion. It was not possible to establish the presence of any membrane separating the vein from the ganglion. Thus it seems that the anterior region of the chamber for a very short distance consists of the confluent pars ganglionaris and pars jugularis, and that in this region the head vein is lateral to the facial ganglion. Here the vein is surrounded laterally and ventrally by the pro-otic bone, and dorsally by the wall of the auditory capsule and the septum semicirculare anterius. Posteriorly to this confluent region of the chamber, the inner bony partition of the pro-otic bone is met with, separating the chamber into two parts as described above. Here bone is also formed in the perichondrium of the septum semicirculare anterius; thus the pars jugularis forms a complete bony canal—the jugular canal—in the pro-otic bone through which the head vein runs (figs. 14, 15, *jc*). A little rostrally to the anterior basi-capsular commissure, this bony canal is pierced in its medial wall, which faces the facial ganglion, by a foramen internum to allow the n. hyoideus facialis (which is distinct and quite separate from

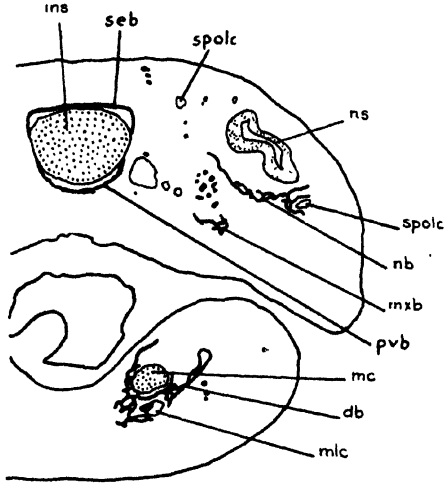

FIG. 4.— *Gymnarchus niloticus*. (15-day larva), T.S. passing through the nasal sacs.

the n. mandibularis facialis, there being no common truncus hyomandibularis as explained on p. 462 of this paper) to enter the jugular canal from the pars ganglionaris. The hyoidean nerve crosses the head vein ventrally and emerges through a foramen externum (fig. 16, *feh*) in the lateral wall of the jugular canal which faces the inner side of the hyomandibular cartilage. The foramen internum is a little anterior to the foramen externum, consequently the hyoidean nerve passes right across the width of the jugular canal slightly diagonally and, therefore, does not run alongside the head vein within the canal. This is in contrast to other teleosts in which, if there is a jugular canal, the common hyomandibular trunk after entering this canal, runs caudally alongside the head vein and passes out through the posterior opening of the canal together with the head vein (*Salmo*, de Beer, 1927). Immediately opposite and medially to the foramen externum, the cartilaginous anterior basi-capsular commissure (fig. 16, *abc*) begins, in direct continuity with the bony inner lamina of the pro-otic which anteriorly separated the jugular canal from the pars ganglionaris. The foramen externum is not small like the foramen internum but is extended longitudinally so that the outer side wall of the jugular canal running

parallel to the anterior basi-capsular commissure is open for a considerable distance posterior to the exit of the hyoidean nerve. But when that region of the commissure is reached where a central area of the cartilage has been eroded, and which consequently consists of only thin perichondral bony lamellae, the side wall appears again (fig. 17). The re-formed bony jugular canal runs posteriorly and opens near the posterior edge of the anterior basi-capsular commissure, anteriorly to the extra-cranial ganglionic swelling of the 9th nerve. The bony lamella of the side wall of the canal facing the hyomandibular cartilage does not, however, stop at the posterior opening of the canal, but extends a short distance caudally until the ventral ridge of cartilage (*vrc*, fig. 18), hanging down from the base of the auditory capsule, is reached. It is evident from this description that the posterior opening of the jugular canal, at the 15th day stage, is not a circular aperture but is rather ill-defined in outline. The space between the above-mentioned bony extension of the side wall of the jugular canal posterior to its opening and the hyomandibula and the base of the auditory capsule, together with the space between the ventral ridge of cartilage (*vrc*) and the hyomandibula, forms a continuous longitudinal inverted groove and is important since it contains some blood-vessels and nerves (see p. 468) which will be referred to later on.

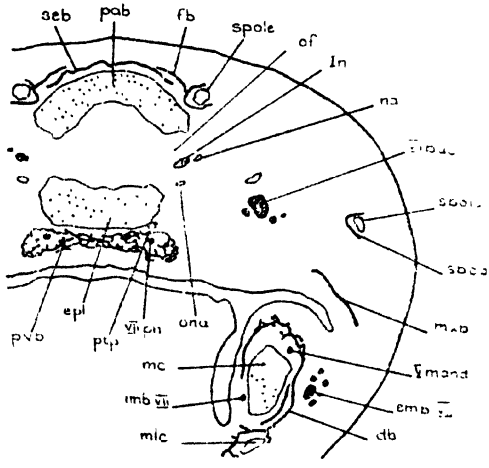

FIG. 5.—*Gymnarchus niloticus*. (15-day larva), T.S. passing through the olfactory foramina.

de Beer (1927) has shown that the outer side-wall of the pars jugularis in those teleosts which possess this structure, consists, in the chondrocranium, of the lateral commissure, which is mainly formed from the fusion of three processes: (*a*) the pro-otic process, (*b*) the post-palatine process, (*c*) to some extent a part of the rudimentary basi-trabecular process. When ossification sets in the cartilage of the lateral commissure is replaced by the outer lamella of the pro-otic bone. In both the present stages of *Gymnarchus*, ossification of the pro-otic is already sufficiently advanced. Vestiges of cartilage embedded in the bony outer wall of the jugular canal in the region anterior to the anterior basi-capsular commissure can be identified as representing the reduced portions of the cartilaginous lateral commissure of earlier stages (fig.14, *ppp*; fig. 15, *pop*). It is also important to note that the external side wall of the jugular canal does not consist solely of replaced bone. That in front of the foramen externum hyoideus is formed in the cartilage of the lateral commissure, that behind this foramen is formed in connective tissue (fig. 17). Here the side wall consists of a single bony lamella extending in the mesenchyme but attached at one end to the outer perichondrium of the base of the auditory capsule.

(f) *The Ethmoid Region.*

The nasal sacs (fig. 4, *ns*) are very moderately developed and are unsupported and far removed from the cartilage of the ethmoid region. The trabecula communis passes imperceptibly into the ethmoid plate. In front of the large olfactory foramina is an internasal septum equal in breadth to the ethmoid plate ; hence in this region the septum and the plate are indistinguishable from each other. The combined internasal septum and the ethmoid plate are produced for a considerable distance anteriorly into the so-called rostrum. The paraphysial cartilage, which chondrifies independently in earlier stages of development, as figured and described by Assheton (1907, Pl. xx, fig. 48, *pc*) in a 9-day larva, has now grown extensively and fused anteriorly with the dorsal hind edge of the transversely broad internasal septum and laterally with the dorsal edges of the orbital cartilage. The side wall of the chondrocranium in the region behind the olfactory foramen is formed by the pre-optic root

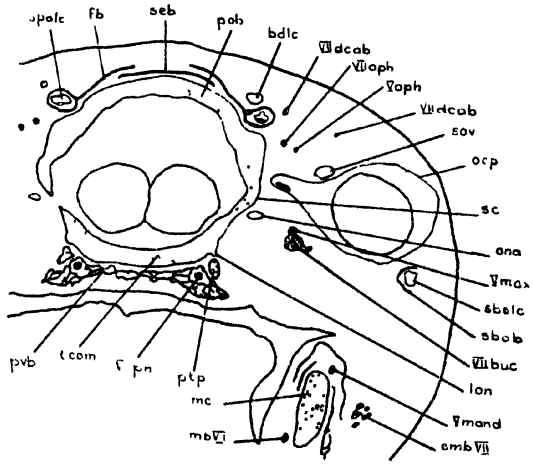

FIG. 6. —*Gymnarchus niloticus.* (15-day larva), T.S. passing through the region between the olfactory foramen and the pre-optic fontanella.

of the orbital cartilage. The olfactory foramen (fig. 1, *of*) is separated by a narrow strip of cartilage from a pre-optic fontanelle (*pf*) which is found in the anterior region of the orbital cartilage. This strip or bridge of cartilage is a part of the pre-optic root of the orbital cartilage. Like the remainder of the pre-optic root it is posterior to the olfactory nerve, lateral to the brain and medial to the orbito-nasal artery and 5th and 7th ophthalmic nerves (fig. 6, *sc*). The lamina orbito-nasalis (figs. 1, 7, *lon*) is in the form of a rudimentary ledge growing from the lateral edge of the fusion of the pre-optic root and the trabecula communis. The pre-optic roots of both sides are wide apart, being separated by the width of the trabecula communis ; the brain extends right forward and the olfactory nerves pass out directly through the olfactory foramina.

(g) *The relations of the Nerves, and Blood-vessels to the Chondrocranium.*

(i.) *Nerves* :—The following description of the nerves of *Gymnarchus* is more than a brief statement of their relations to the cartilages of the chondrocranium. Since the facial nerve of larval *Gymnarchus* has proved to be very interesting in the number and disposition of its branches, it is considered here in some detail. The present study, however, does not pretend to be more than a broad account of the nerve sufficient for the understanding and identification of its branches before describing

their relations to other structures. The nerves as they originate from the facial ganglion are considered to some extent, but not all their subsequent branches are included.

The olfactory nerve (fig. 3, *I n*) as it leaves the olfactory foramen is accompanied by the nasal artery (*na*) which is a branch of the orbito-nasal artery (*ona*). The nasal artery crosses the nerve laterally and runs along dorsally with it.

The optic nerve (*II n*) passes out from the optic foramen accompanied by the arteria centralis retinae (*acr*); together they run forward in an antero-dorsal direction, passing medially to the orbito-nasal artery, to the maxillary ramus of the 5th nerve and to the buccal ramus of the 7th nerve.

The oculomotor and the trochlear nerves (fig. 3, III *n*, IV *n*) leave the cranial cavity through a common foramen in the metoptic root of the orbital cartilage. The two nerves in their forward course are soon accompanied by the abducens nerve, which emerges through the pro-otic foramen medially to the common trunk of the ramus maxillaris trigeminus and the ramus buccalis facialis (fig. 12, *VI n*). All the three nerves for the eye-muscles run close together one above the other, and for some distance they are covered laterally by the common trunk just mentioned (figs. 9, 10).

All the branches of the trigeminal and the facial nerves, except the palatine, the pre-trematic, and the hyoidean divisions of the facialis, emerge through the large

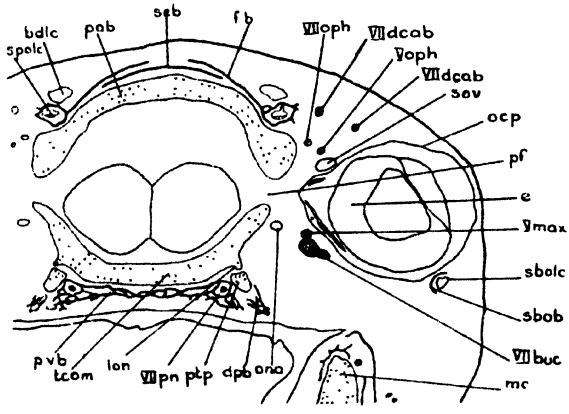

FIG. 7.—*Gymnarchus niloticus*. (15-day larva), T.S. passing through the pro-optic fontanellae.

pro-otic foramen. The ophthalmicus trigeminus (fig. 3, *Voph*) runs forward dorsally to the superior orbital vein (*sov*) ventrally to the pituitary vein (*pv*) and its foramen, laterally to the "posterior branch of the anterior artery" (*Pbaa*) and ventrally to the foramen for the anterior cerebral vein, but laterally to this vein (*acr*) itself. The maxillary branch of the trigeminal nerve (*Vmax*), very soon after it leaves the trigeminal ganglion, comes close to, and runs dorso-medially associated with, the buccalis branch of the facial (*VII buc*) as a common trunk, which during its forward course passes along laterally to all the principal arteries and other nerves in its neighbourhood.

The ramus mandibularis V (*Vmand*), which arises from the trigeminal ganglion very close to the ramus maxillaris V, comes out through the pro-optic foramen closely associated with ramus buccalis VII, at first medially, then ventrally. In fact these three nerves emerge through the pro-otic foramen as a common trunk and run in this manner or a short distance in their forward course (fig.12). In the accompanying reconstruction (fig. 3) this region has been represented diagrammatically for the sake of clarity. The mandibular branch of the 5th nerve subsequently crosses the palatine nerve (*VII pn*) and the palatine artery (*pna*) laterally.

Other branches of the 7th nerve are :—

(i) The ophthalmic (*VII oph*), which is quite distinct from the ophthalmic branch of the 5th nerve, and runs forward clearly separated from it and dorsally to the foramina for the pituitary and anterior cerebral veins.

(ii) The otic (*VII ot*), which arises from the facial ganglion close to the origin of the ophthalmicus facialis.

(iii) The buccal (*VII buc*), a massive nerve which, as already described, passes laterally to the mandibular ramus of the 5th nerve, and runs along the maxillary ramus of the same nerve, partly overlapping it laterally (figs. 8 to 12).

The truncus hyomandibularis facialis communis of other fishes is in *Gymnarchus* completely split up into two components—the n. mandibularis facialis and the n. hyoideus facialis—which leave the skull through different foramina. The ramus opercularis superficialis facialis, which is the third principal branch of the truncus hyomandibularis communis is, in *Gymnarchus*, only partly associated with the n. mandibularis facialis.

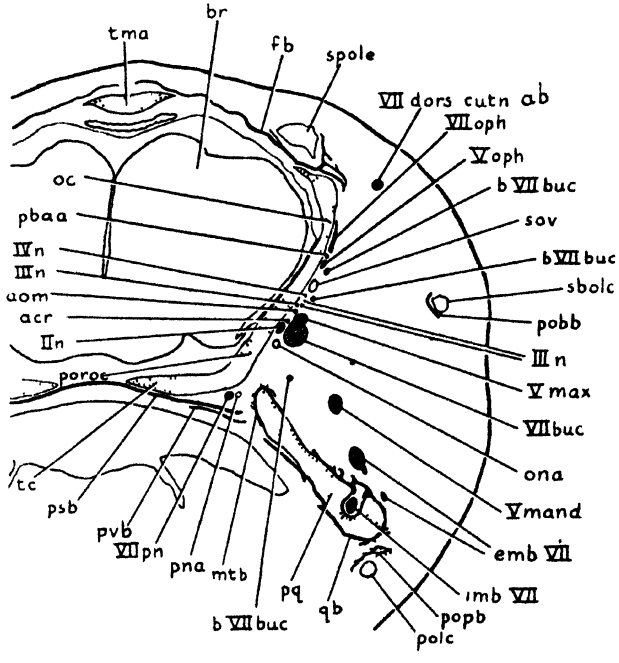

FIG. 8.—*Gymnarchus niloticus*. (15-day larva), T.S. passing through the foramen in the quadrate for the internal mandibular nerve, and slightly anterior to the epiphysial bar.

The n. mandibularis facialis (fig. 3, *VII mand*) issues from the geniculate ganglion by a distinct root close to the origin of the n. buccalis facialis and comes out through the pro-otic foramen near its ventral border. It passes laterally to the carotid artery and runs forward laterally to the pterygoquadrate cartilage (figs 9, 10). It gives out quite a number of branches before it reaches the foramen in the quadrate where it divides into the ramus manibularis internus and the ramus mandibularis externus (fig. 8). The ramus internus enters this foramen and runs anteriorly, remaining medial to Meckel's cartilage.

The n. hyoideus facialis (fig. 3, *VII hyoid*) is the most posterior nerve to arise from the geniculate ganglion. As already shown it enters the jugular canal from the

pars ganglionaris through the foramen internum in the bony partition between the two parts. Within the jugular canal it crosses the head vein ventrally and leaves through the foramen externum in the outer lateral wall of the canal. Now it runs, remaining dorsal to the m. adductor mandibularis, towards the hyomandibula, the inner surface of which it pierces and comes out through a foramen on its outer surface. From here it runs between the hyomandibular cartilage and the preopercular bone (fig. 16) before it reaches the ventral position where it divides into its different rami. Where it is ventral to the head vein in the jugular canal, the hyoidean nerve gives out a slender branch—the ramus opercularis profundus facialis—which runs posteriorly, first ventrally, then laterally to the head vein in the jugular canal, remaining close to the mouth of the longitudinally reduced foramen externum, through the hind limits of which it comes out. This nerve is the motor nerve of the m. adductor

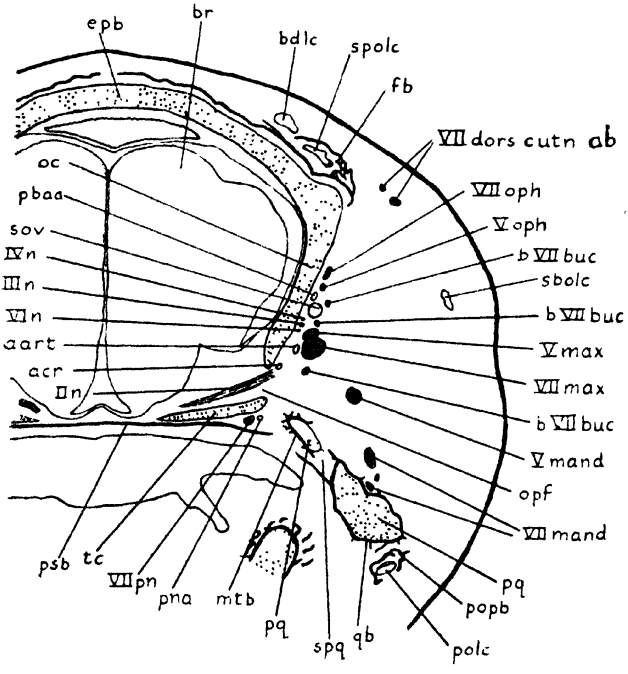

FIG. 9.—*Gymnarchus niloticus*. (15-day larva), T.S. passing through the anterior region of the optic foramen, the space in the pterygoquadrate and the epiphysial bar.

operculi and is in part homologous with the similarly named nerve in *Menidia* described by Herrick (1899). Before reaching the muscle, which lies far back from the exit of the nerve through the foramen externum, this nerve runs through the passage which, as already explained, lies between the hyomandibula, the posterior extension of the bony lateral wall of the jugular canal, the base of the auditory capsule and the adductor muscle of the mandible, and posteriorly between the hyomandibula and the vertical lamina of cartilage (figs. 17, 18, *VII operc. prof*).

The n. opercularis superficialis facialis (*VII operc.super*, fig. 3) which in other fishes branches out from the truncus hyomandibularis facialis far away from the geniculate region originates in *Gymnarchus* almost as an independent nerve. Its root, which originates from the geniculate ganglion in the area between the origin of the mandibular, dorsal cutaneous, and palatine branches, is only partly associated

with the root of the mandibular branch. It also receives a considerable number of fibres from the root of the dorsal cutaneous branch. The n. opercularis superficialis facialis leaves the skull through the pro-otic foramen and pierces the medial side of the anterior region of the hyomandibula which is dorsally ossified in this region, and issues through a foramen on the outer side of the hyomandibular bone, and then divides posteriorly into two branches. One branch enters the bony canal in the pre-opercular bone, which lodges the middle part of the pre-opercular latero-sensory canal, and the other branch runs external to the pre-opercular bone and sends branches to this bone and also some branches to the glandular organs of the skin in the vicinity of the pre-opercular bone.

The palatine nerve (fig. 3, *VII pn*) arises from the geniculate ganglion by an independent and distinct root (fig. 13), which pierces the pro-otic bone through a

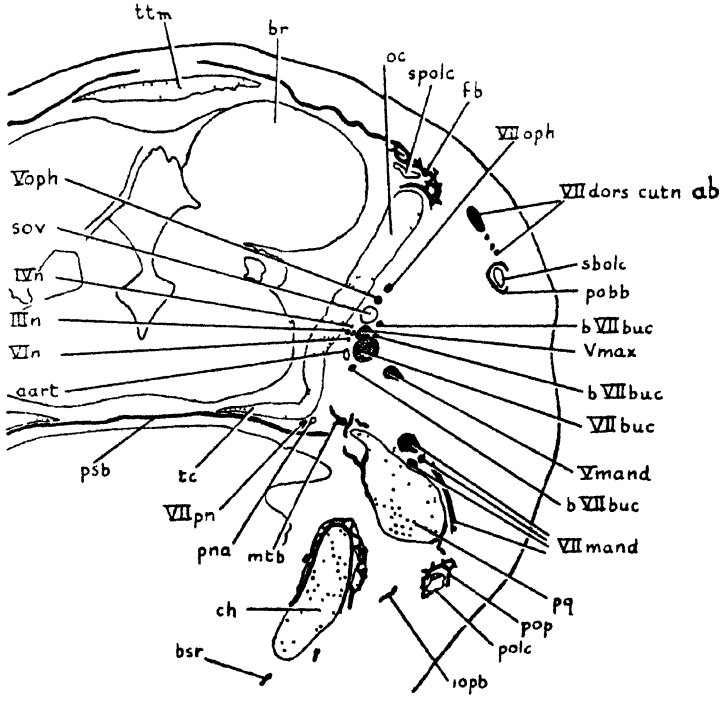

FIG. 10.—*Gymnarchus niloticus*. (15-day larva), T.S. passing through the pila metoptica and anterior to the line of fusion of the quadrate with the hyomandibula.

foramen ventrally to the ganglion. It runs forward ventrally to the lateral edge of the trabecula for a short distance where it is at first dorso-lateral and then lateral to the internal carotid artery, dorsal to the lateral edge of the parasphenoid bone and medial to the palatoquadrate. Soon it shifts its position dorsally and becomes lateral to the metoptic root of the orbital cartilage. Here it occupies a position medial to the pterygoquadrate between the intramembranously ossifying lamellae of pro-otic bone and the metoptic root (fig. 12). After a short distance the palatine nerve again slips down running ventro-laterally along the line of the fusion of the metoptic root with the trabecula and dorsally to the parasphenoid bone (fig. 10). From the optic foramen onward, the nerve becomes ventral to the trabecula and runs between it and the parasphenoid (fig. 9). Anteriorly, in the region of the prevomer, the palatine nerve runs in a complete bony canal (figs. 5 to 7) in the lateral

margin of this bone. A little distance anteriorly to the olfactory foramen this canal opens by means of a lateral foramen which gives exit to the palatine nerve. Thus the palatine nerve in its entire course remains medial to the palatoquadrate. Between the origin of the palatine nerve and the n. opercularis facialis, a delicate nerve originates from the geniculate ganglion and pierces the pro-otic bone laterally to the foramen for the palatine nerve. This delicate nerve was traced through the connective tissue between the pro-otic bone and the roof of the mouth. It seems that this nerve represents in part the ramus pre-trematicus facialis of *Menidia* described by Herrick (1899). This nerve in *Menidia* innervates the mucosa of the roof of the mouth and the pseudobranch. It was not possible to trace the finer branchings of this nerve in *Gymnarchus* as they soon became lost in the mesenchyme. There is no pseudobranch in *Gymnarchus*; therefore, this nerve of *Gymnarchus* represents in part the ramus pre-trematicus facialis of *Menidia*.

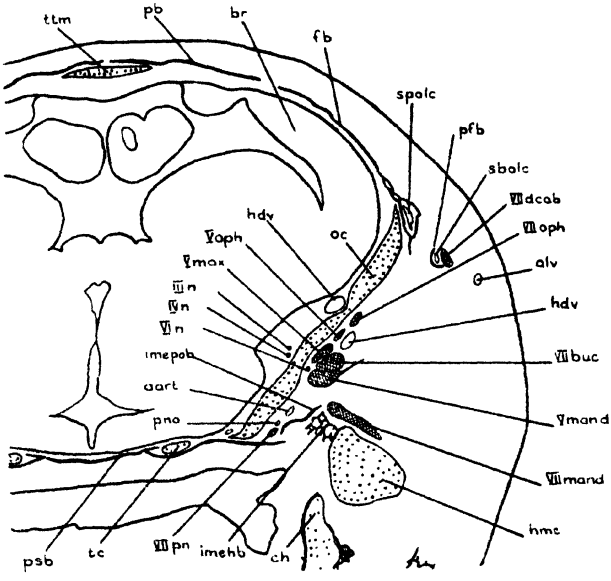

FIG. 11.—*Gymnarchus niloticus*. (15-day larva). T.S. passing between the common foramen for the III and IV nerves and the pituitary vein foramen. The plane of the section is just posterior to the hind limit of the line of fusion of the quadrate with hyomandibula.

A very prominent and stout nerve originates from the geniculate ganglion dorsally to the origin of the palatine nerve. This nerve leaves the skull through the pro-otic foramen and loops under the head vein ventrally and laterally; it then passes over the outer wall of the auditory capsule (fig. 13, *VII dors.cutn*). For this stout nerve I propose the name: "dorsal cutaneous facial", or ramus *sive* nervus dorsalis cutaneus facialis (fig. 3, *VII dors.cutn*). The dorsal cutaneous facial trunk divides into three branches—one ventral and anterior, and one posterior. Before the main nerve trunk passes over the outer wall of the auditory capsule to divide into the anterior and posterior branches, the ventral branch is given off (not shown in fig. 3). This branch first runs towards the lateral surface (fig. 13, *VII dcvb*) and then reaching near to the skin bends down ventrally. The ventral branch gives rise to quite a number of secondary branches, almost all the nerve-twigs from which ultimately supply the so-called multicellular glandular organs of the skin of the operculum and neighbouring regions. The posterior branch (fig. 3, *pbdc*) gives off many branches,

most of which innervate the multicellular glandular organs of the skin of the auditory region. The anterior branch (*abdc*) runs rostrally giving off many smaller branches in its course, almost all of which innervate the glandular organs of the skin in the dorso-lateral and dorsal regions of the orbitotemporal part of the head ; ultimately this nerve reaches the ethmoid region and divides into many branches which innervate the glandular organs of the skin of this region.

Consideration of the details of the various nerves is beyond the scope of this paper, moreover, a critical and definitive study in this field cannot be undertaken on isolated larval stages stained by ordinary routine laboratory methods. Therefore, only certain significant points with regard to this peculiar nerve will be treated here.

The anterior branch of the dorsal cutaneous trunk is roughly parallel with the nerve I have designated n. ophthalmicus superficialis facialis in the reconstruction, but these two nerves are not in the same longitudinal vertical plane ; the n. ophthalmicus superficialis facialis is in a more medial plane, very near to the side wall of

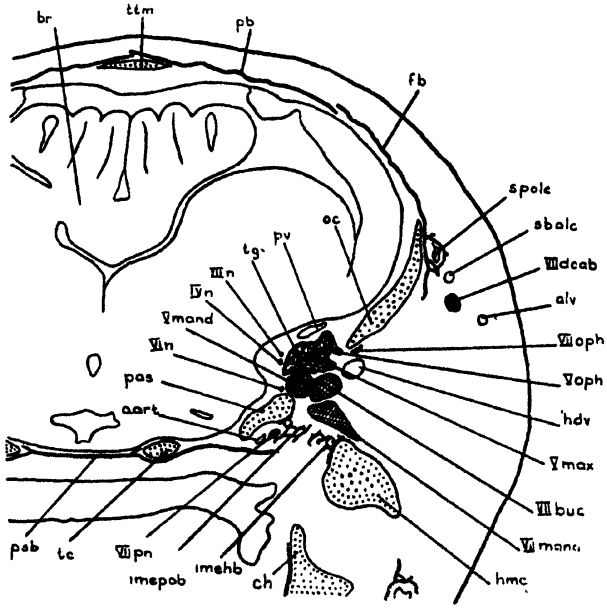

FIG. 12.—*Gymnarchus niloticus*. (15-day larva), T.S. passing through the anterior region of the pro-otic foramen.

the chondrocranium, whereas the other nerve runs in a much more lateral plane, far removed from the side wall of the skull and from the n. ophthalmicus superficialis facialis (figs. 8 to 11). The posterior branch of this trunk, so far as I could make out, is not equivalent to the dorsal recurrent branch of the facialis, with which a similar branch of the vagus combines to form the ramus lateralis accessorius (Goodrich, 1930) in certain teleosts. I have not been able to establish any connection between this nerve and the vagus. No branch from either the anterior or the posterior or the ventral divisions of this trunk innervates any lateral line sense organ of the head, though both these nerves during their course, run at some places very close to the lateral wall of the sensory canal (figs. 11, 18). The most important fact is that the dorsal cutaneous trunk originates from the geniculate ganglion ventrally to the head vein whereas the nn. ophthalmicus trigeminus, ophthalmicus facialis and oticus facialis originate dorsally to this vein (figs. 12, 13).

As regards the two ophthalmic nerves it can be seen that two distinct nerves—n. ophthalmicus trigeminus and n. ophthalmicus facialis—are identified in the accompanying reconstruction (fig. 3). Holmgren (1943) while describing the orbital capsule of larval *Gymnarchus* gives a microphotograph of a section (his fig. 84, p. 178) in which these two distinct nerves are labelled together as the "nervus ophthalmicus superficialis VII". I have, however, followed the course of these nerves carefully, and from the foregoing description of their relations to other structures there is no doubt that they are different nerves.

I was not able to distinguish a nervus profundus. It cannot be regarded as fused with the n. ophthalmicus trigeminus since the latter nerve is dorsal to the oculomotor nerve.

The glossopharyngeal nerve is described in the section where the relation of the air-bladder diverticulum to the ear is considered.

The vagus nerve comes out through the metotic or jugular foramen between the occipital arch and the auditory capsule.

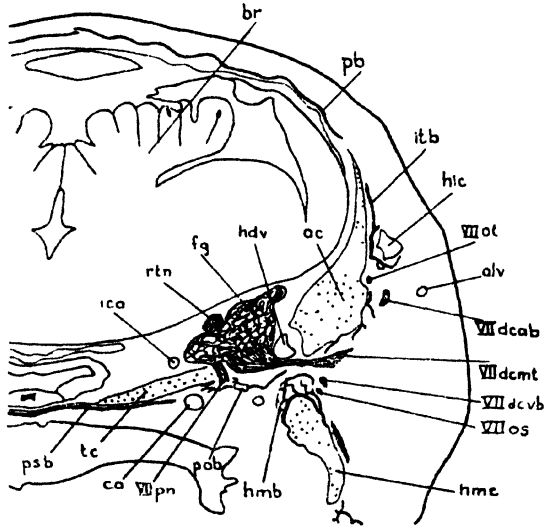

FIG. 13.—*Gymnarchus niloticus*. (15-day larva), T.S. passing through the posterior region of the pro-otic foramen, showing the origin of the nn. palatinus et dorsalis cutaneus VII.

(ii.) *Veins*.—The blood from the ethmoid region of the head is ultimately conveyed into a large vein—the superior orbital vein (fig. 3, *sov*) which runs caudally, ventrally to the n. ophthal. trigeminus and dorso-medially to the orbital capsule. In the orbitotemporal region the superior orbital sinus receives the following main tributaries: (*a*) the anterior cerebral vein (*acv*), which comes out through its foramen and passes medially to the n. ophthal. trigeminus, (*b*) a vein (*iov*) coming out of the posterior conical end of the orbital capsule where the recti muscles are grouped together (perhaps this vein represents the inferior orbital vein of other forms described by de Beer, 1924), and (*c*) the pituitary vein (*pv*) which comes out through its foramen in the pila antotica secundaria and passes laterally to the n. ophthal. trigeminus. From this point backwards the superior orbital sinus is the main vein of the head and is designated as the head vein (*hdv*). The head vein runs along the pro-otic foramen lateral and very close to its opening and eventually in the posterior part of the foramen it dips into the opening and enters the trigemino-facialis chamber in the manner already described. Emerging from the posterior opening of the jugular canal, it runs laterally to the glossopharyngeal nerve and medially to the vertical

ridge of cartilage (fig. 18, *v.rc*) which hangs down from the base of the auditory capsule. A short distance behind this region the head vein receives a big vein, which is the main vein (not shown in fig. 3) of the opercular region. This vein is formed by the union of various veins, chief among which are those coming from the four opercular bones and the ceratohyal. In the region of the vagus nerve the head vein runs medially to the branches of this nerve. No vena capitis lateralis is present in this region, neither is there any indication of any venous loops from the head vein around any of the vagal branches. The posterior cerebral vein issues through the jugular foramen along with the vagus nerve, to which it is lateral, and then turns medially to join the head vein.

A short distance posterior to the exit of the hyoidean nerve through the foramen externum in the lateral wall of the jugular canal, a vessel of moderate size but having an extremely thin lining, opens into the lateral aspect of the head vein. As its course justifies, I propose to call it the " anterior lateral vein ". Its course may now, briefly, be considered. It joins the head vein within the jugular canal dorsally to the opercular artery and to the n. opercularis profundus facialis. After coming out of

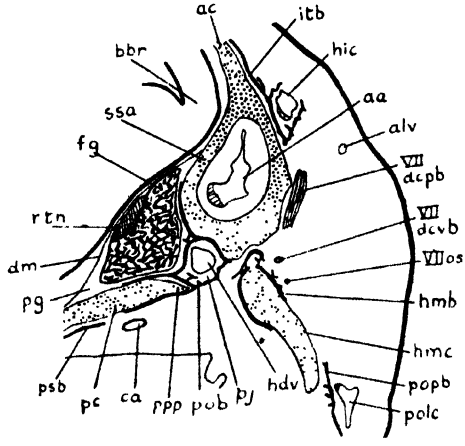

FIG. 14.—*Gymnarchus niloticus*. (15-day larva), T.S. passing through the trigemino-facialis chamber, showing the cartilaginous remains (corresponding to the postpalatine process of earlier stages) in the bony lateral commissure which forms the latero-ventral side-wall of the pars jugularis.

the foramen externum hyoidei, the anterior lateral vein runs posteriorly within the space in which the n. opercularis profundus facialis runs as already described (figs. 17, 18, *alv*). Thus for a considerable distance this vein is medial to the hyomandibula. It crosses the opercular vein, which comes from the lateral side to join the head vein, running ventrally to it and then immediately turns in a postero-lateral direction until it comes near the skin. From here the anterior lateral vein takes a sharp antero-dorsal turn and runs between the skull and the skin. Its anterior course was followed up to the middle of the orbito-temporal region, where it became lost in the very loose mesenchyme and could not be traced further.

During its course the anterior lateral vein receives many small tributaries. The anterior lateral vein and all its tributaries are entirely devoid of blood corpuscles. Their walls are thinner than those of other veins of similar size. The anterior lateral vein and its tributaries form a system of their own and never open into other venules even where their walls come into intimate contact with each other. The anterior lateral vein is not comparable to the " extra vein " of *Cottus bubalis* (de Beer, 1924) which joins the orbital sinuses in front, and running laterally to the hyomandibula

joins the vena capitis lateralis and the secondary vein in the region of the glossopharyngeal nerve, which of course, unlike *Gymnarchus*, is far behind the hyomandibula. Thus the extra vein is not medial to the hyomandibula in any part of its course. The anterior lateral vein of *Gymnarchus* is in part medial to the hyomandibula and in part lateral. It is dorsal to the adductor of the mandible.

(iii.) *Arteries.*—There are two lateral dorsal aortae (fig. 3, *ila.ola*) on each side, parallel to each other. The outer one is formed by the union of the third and fourth different branchial vessels, and running caudally joins with its fellow of the opposite side. The common trunk thus formed immediately breaks up into the coeliaco-mesenteric artery and the artery for the air-bladder. The inner and more anterior aorta is formed on each side by the union of the first and second efferent branchials. The inner lateral aortae unite posteriorly to form the median dorsal aorta; a vessel, however, is present establishing a connection between it and the above mentioned common trunk. This description is based on Assheton's work p. 339). What follows is new and was not considered by him.

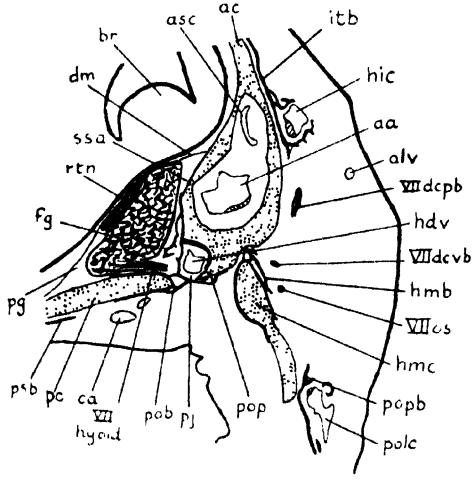

FIG. 15.—*Gymnarchus niloticus*. (15-day larva), T.S. passing through the trigemino-facialis chamber (a little posterior to fig. 14), showing the cartilaginous remains (corresponding to the pro-otic process of earlier stages) in the bony lateral commissure.

The carotid artery, on each side, is the direct prolongation of the inner lateral aorta. It runs below the basal plate, medially to the head vein. Anterior to the auditory region it comes near the outer edge of the trabecula, passing medially to the palatine foramen (fig. 13). Lateral to the trabecula it gives out an internal carotid, which enters the skull through a foramen separated from the hypophyseal fenestra by a strip of cartilage as already described. Further on, from the point of the origin of the internal carotid it is difficult to give the anterior arterial prolongation a name, since the branching of the arteries anterior to this point is totally unlike that of other larval fish and therefore makes the comparison with the arteries of other fish difficult. For the sake of convenience of description it will be referred to as the "anterior artery". Anterior to the origin of the internal carotid the anterior artery comes near the lateral surface of the metoptic root passing medially to the palatine nerve (fig. 12). After having given off a "palatine artery" (fig. 3, *pna*) which runs laterally along the palatine nerve, the anterior artery runs in an antero-dorsal direction and comes near the n. buccalis facialis where it becomes internal and exactly medial to

the nerve (fig. 10, *aart*) for some distance (in this region in the accompanying reconstruction (fig. 3) this artery is shown exposed laterally for the sake of clarity). Here it gives off two branches, one anterior and one posterior. The posterior branch (*pbaa*) is lateral to all the three nerves of the eye muscles but medial to all other structures which it crosses during its forward course. The anterior branch runs ventrally to the abducens nerve and enters the posterior cone of the orbtial capsule along with other blood vessels and nerves. I have recognized this artery as the arteria ophthalmica magna fig. 3, *aom*). The rest of the " anterior artery " after giving off these two branches becomes the orbitonasal artery (*ona*). Underneath the auditory capsule the carotid artery gives off an opercular artery which sends, anteriorly, a branch to the hyomandibular and quadrate cartilages and then runs back in the passage in which the nerve for the m. adductor operculi (*VII oper.prof*, figs 17, 18) and the " anterior lateral vein " run. Ultimately the artery supplies this muscle and also sends some branches to the preopercular bone.

(h) *The relation of the Air-bladder to the Chondrocranium.*

Some confusion about the relations of the air-bladder to the ear and to the lateral line canal exists in the literature. Allis (1904), whose statement is based on a

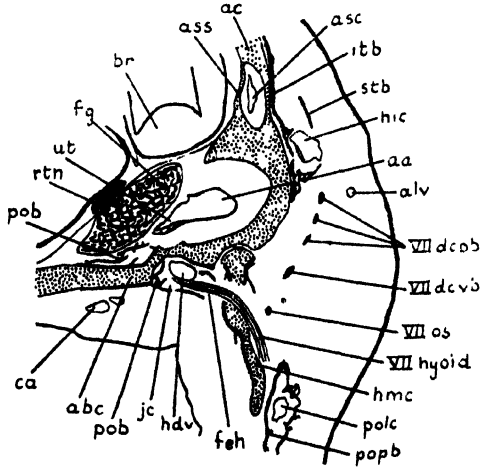

FIG. 16.—*Gymnarchus niloticus*. (15-day larva), T.S. passing through the foramen externum hyoideus in the jugular canal.

dissection of adult specimens regards the sac-like structure lodged within the auditory capsule in opposition to the lateral vacuity in the outer wall of the capsule as a " balloon-like distension of the non-sensory portion of the sacculus . . . ". Assheton (1907) refutes Allis's description and shows that the sac is a diverticulum from the air-bladder, which in early stages grows forward and enters the auditory capsule, but in later stages the connection between the inflated diverticulum and the air-bladder is lost. F. M. Ballantyne (1927) confirms Assheton in the derivation of the auditory diverticulum from the air-bladder. She also maintains that the connection is lost in later stages, but she has not taken into consideration the subsequent relations of the sac to the ear and other surrounding structures. In the present two stages the condition is as follows.

From the anterior end of the air-bladder a duct runs anteriorly and afterwards bifurcates. Each branch, which may be called the cylindrical diverticulum, runs between the two lateral aortae of either side, below the basioccipital bones. Soon the cylindrical diverticulum enters a canal in this bone. The inner side of this bony canal consists of the perichondral ossification in the lower portion of the occipital

arch ; the external side is formed by intramembranous extensions of bony lamellae. The bony canal lodging the cylindrical diverticulum of the air-bladder, shifts its position somewhat laterally and attains similar relations with the ossifying exoccipital bone, i.e. one side surrounded by perichondral ossification and the other by intramembranous bony extensions. The exoccipital bone continues in the posterior part of the auditory capsule (there is no opisthotic ossification). After passing under the posterior basi-capsular commissure the bony canal opens into the cavity of the auditory capsule into which the diverticulum enters. Here the cylindrical diverticulum is dorsal to the intramembranously ossifying floor of the basi-capsular fenestra, and medial to the bony partition ossifying in the membrane between the utriculus and sacculus shortly to be described. Eventually the diverticulum passing ventrally to the saculo-lagenar canal, opens into the posterior ventral aspect of a distended

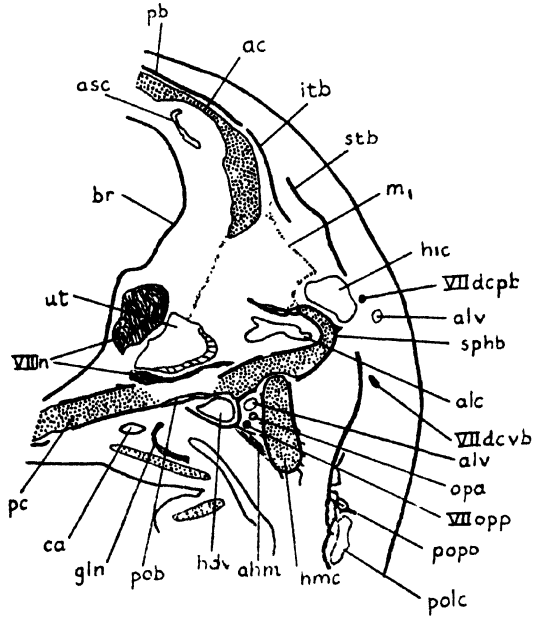

FIG. 17.—*Gymnarchus niloticus*. (15-day larva), T.S. passing through the anterior region of the lateral vacuity in the auditory capsule.

sac (fig. 19), whose histological structure is essentially the same as that of the diverticulum. Thus this sac is the direct anterior extension of the air-bladder. The sacculus is closely opposed to a part of the medial wall of the distended sac (figs. 18, 19) but the walls of both, which are in intimate contact, are easily distinguishable from one another.

The membranous labyrinth has itself undergone interesting modifications (Assheton, 1907). The sacculus is not directly under the utriculus in the same vertical plane but is located laterally to the utriculus. A delicate canalis reuniens joins the two. The junction between the sacculus and the lagena is also narrowed down into a sacculo-langenar canal, which, however, is shorter in length than the canalis reuniens. Assheton makes no mention of this canal, nor of a delicate membrane which is located between the utriculus and the sacculus. This membrane is partly ossified, especially in its posterior part. In the younger embryo this posterior intramembranous ossification is not continuous with the perichondral ossification of the exoccipital, which has usurped the place of the opisthotic of other forms. But in the 15th day stage the two ossifications have become continuous.

This membranous ossification has also extended between the utriculus and the sacculus. It is evident that gradually the entire membrane would become ossified together with the otic bones, leaving however, foramina for the passage of nerves, etc., thus leading to the adult condition where the cavity of the auditory capsule is divided into two chambers which have been described in detail by Allis (1904). The inner chamber lodges the utriculus and the outer one the sacculus, the lagena, and the inflated sac, which is a derivative of the air-bladder and not of the sacculus as Allis had regarded it. The posterior part of the lagena pushes into the exoccipital bone ; thus the outer lateral chamber has a posterior blind extension into this bone. The beginning of this condition is already evident in the present two larvae. The vesicular diverticulum of the air-bladder occupies a position between the anterior part of the lagena and the sacculus on one side and the horizontal semicircular canal on the other, rising up above the level of the canal and occupying the inner extent of the lateral auditory vacuity. As already described, this vacuity is covered by a membrane, lateral to which are the temporal and supratemporal latero-sensory canals, which are covered externally by the supra-temporal bone.

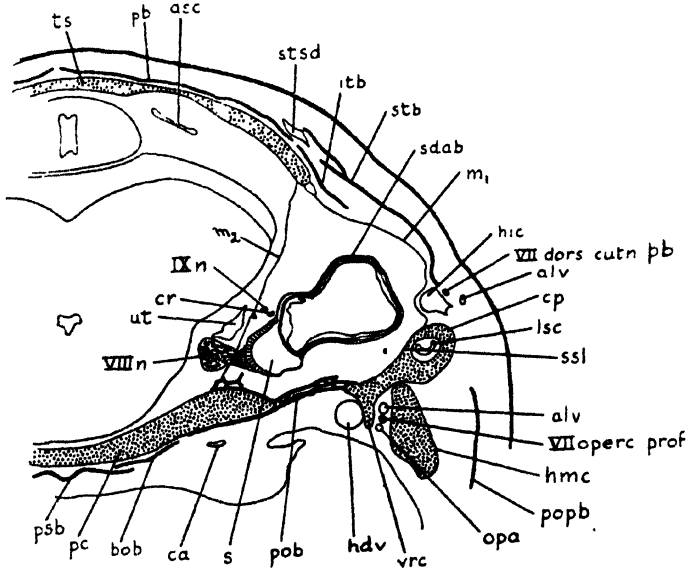

FIG. 18.—*Gymnarchus niloticus*. (15-day larva), T.S. showing the relation of the auditory diverticulum of the air-bladder to the ear.

The relations of the glossopharyngeal nerve to the auditory capsule can now be considered more appropriately. Fig. 19 is a diagrammatic representation of the ear and the auditory diverticulum of the air-bladder of *Gymnarchus* ; the course of the glossopharyngeal nerve is also shown. For the sake of clarity the auditory nerve is omitted. The dorso-ventral overlapping of the various structures has been reduced to a minimum by stretching the structures medio-laterally in the diagram.

After issuing from the brain the glossopharyngeal nerve runs ventrally to the utriculus, crosses the canalis reuniens first ventrally then runs laterally along with it and then passing dorsally over the canalis runs medially to it. The nerve and the canalis reuniens together perforate the membranous partition (here showing early stages of ossification) located between the utricle and the saccule. From here the nerve runs dorsally to the saccule, traverses the space between the anterior parts of the saccule and the diverticulum of the air-bladder, and eventually enters a foramen

in the bony base of the auditory capsule behind the anterior basi-capsular commissure. The supratemporal branch of the glossopharyngeal nerve crosses the canalis reuniens ventrally and after perforating the membranous partition (here ossified) runs dorsally to the lagena. It ultimately leaves the skull through a foramen in the exoccipital bone, which here occupies the place of the absent opisthotic. This foramen is anterior to the posterior basi-capsular commissure.

(i) *The relation of the Pterygoquadrate to the Neurocranium.*

Assheton's work (1907) purports to show that the pterygoquadrate in the larval *Gymnarchus* is attached along its entire length to the neurocranium. According to his figure (Pl. xx. fig. 50), in a 43 day larva the pterygoid process of the quadrate is fused anteriorly with the lateral edge of the trabecula communis. Behind this ethmoid fusion, and in continuation with it, Assheton shows an extension of the palato-basal

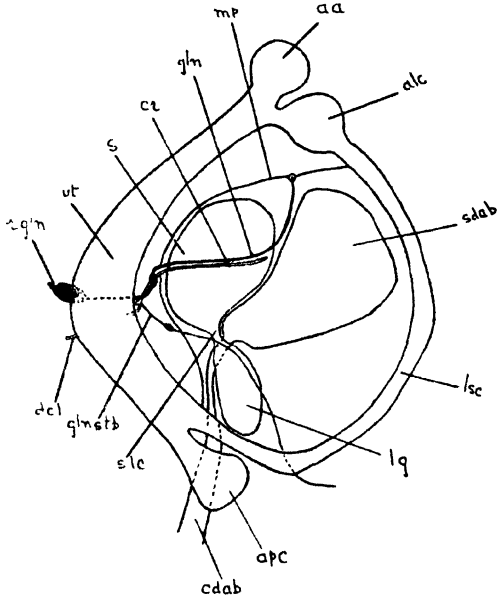

FIG. 19.—Diagramatic representation of the relation of the air-bladder diverticulum to the ear. The course of the glossopharyngeal nerve is also shown. The auditory nerve has been omitted for the sake of clarity.

attachment brought about by the opposition of a well-developed basal process with the lateral edge of the trabecula and posteriorly with the basi-trabecular process of the neurocranium. The broad and long basi-trabecular process he shows as articulating not only with the posterior part of the basal process but also with the anterior part of the hyomandibular cartilage (the posterior part of which is fused with the auditory capsule). The quadrate is also fused with the hyomandibula by pro-cartilage. Thus, if Assheton's findings were correct, the *Gymnarchus* would represent the only known case of a larval teleost having an extreme type of amphistylic jaw suspension.

de Beer (1937, pp. 135, 513) pointed out the necessity of further work on this region so that the precise details of this attachment might lead to a better understanding of this exceptional teleost.

In the two larvae under investigation, the older of which is of a 15-day stage, there is neither the basal nor the basi-trabecular process. Not even a rudimentary indication of these processes is present. Only the ethmoid attachment exists. The

remaining part of the pterygoquadrate is not in any cartilaginous fusion or attachment with the neurocranium. The quadrate is fused posteriorly with the hyomandibula by dense pro-cartilage. Thus it is seen that in a 15-day larva the jaw suspension is quite different from that of a 43-day stage as described by Assheton. One might be led to presume that the 15-day larva represents a stage prior to the development of the basal and basi-trabecular processes, which, after their formation in later stages, might eventually lead to the amphistylic suspension shown by Assheton. The following detailed account of the condition found in the 15-day stage indicates that this conclusion is not tenable, as there is no possibility of the subsequent formation of these processes, since ossifications in the pterygoquadrate and the neurocranium have already started in places whence the basal and basi-trabecular processes would grow if they were present. Assheton's figure, therefore, must be erroneous in showing these processes.

The anterior tip of the pterygoid process is in contact (but not in fusion) with the lateral edge of the trabecula communis. Behind the olfactory foramen the pterygoid process is at first in pro-cartilaginous fusion with the anterior part of the lamina orbitonasalis and then in the posterior part of this lamina it runs closely along the lamina (fig. 7). From behind the posterior limit of the lamina orbitonasalis to a short distance anterior to the foramen for the optic nerve, the pterygoid process laterally runs along the lateral edge of the trabecula, but not so near as it was to the lamina orbitonasalis. A little distance anteriorly to the optic foramen, perichondral bony lamellae of the metapterygoid with intramembranous extensions into the surrounding mesenchyme have developed around the upper edge of the pterygoquadrate (fig. 8, *mtb*). This metapterygoid ossification continues backwards as far as the posterior end of the pterygoquadrate cartilage where the latter is fused to the hyomandibula. It is important to note that nowhere is the developing metapterygoid in contact with any part of the neurocranium. There is no basi-trabecular process, either cartilaginous or of replaced bone. Instead, bony lamellae, which ossify intramembranously and end freely laterally, arise from the perichondrium of the lower part of the pila antotica and of the base of the skull in the region of the pro-otic foramen (fig. 12). These lamellae seem to be in continuity posteriorly with the pro-otic bone (fig. 13); they are opposed to the anterior part of the ossifying hyomandibular bone.

The discrepancies between the conditions of the 43-day stage as exemplified in Assheton's figure and that of the present 15-day larva are not reconcilable in any way. In view of the foregoing the present investigation shows that the pterygoquadrate is not attached to the neurocranium except in the ethmoid region. The jaw suspension in the chondrocranium of *Gymnarchus* is methyostylic and is, therefore, essentially the same as in other Teleostei.

3. Discussion.

Among the Teleostei there is a tendency for the reduction of the cartilage in the chondrocranium. *Gymnarchus*, like *Clyclopterus lumpus*, presents an interesting example of a teleost in which the cartilage of the chondrocranium has secondarily undergone a large degree of development. On the whole the chondrocranium of *Gymnarchus*, save for a few peculiarities, conforms to the generalized Teleostean pattern.

The intramembranous extensions of perichondrial bones, some of which are alluded to in the foregoing pages, are comparable to a great extent to the peri-, epi- and apo-lamellae of *Cyclopterus lumpus* (Uhlmann, 1921). de Beer (1937, p. 495) has amassed and reviewed a large amount of data which show that intramembranous extensions from cartilage bones are by no means uncommon in fishes.

The occipital region of the 15-day larva of *Gymnarchus* does not show any segmentation in the shape of spinal processes in the lateral cartilage of the occipital arch, but the superior occipital cartilage and the presence of three pairs of mixed nerves are definite signs of segmentation in the posterior part of the occipital region.

The three pairs of nerves between the occipital arch and the first vertebra indicate that at least two occipito-spinal vertebrae have become indistinguishably amalgamated in the occipital arch of the 15-day stage. The fact that the superior occipital cartilage is separate from the tectum posterius is of interest. This cartilage is present in those teleosts in which the anterior vertebrae take part in the formation of the Weberian ossicles. In *Cyprinus carpio*, according to Nusbaum (1908), the neural spine of the third vertebra, which takes part in the formation of the claustrum and scaphium, fuses with the tectum posterius and gives rise to the superior occipital cartilage. In *Amiurus*, according to Matveiev (1929), the neural spines of the first and second vertebrae appear to form the superior occipital cartilage which connects the tectum posterius with the third vertebra. In other Ostariophysi hitherto investigated—*Ictalurus* (Ryder, 1887), *Callichthys* (Ballantyne, 1930), *Scardinius* (Matveiev, 1929), *Leuciscus* (Hubendick, 1942)—this cartilage is always formed. *Gymnarchus* has no Weberian apparatus and is not closely related to the Ostariophysi. The superior occipital cartilage of *Gymnarchus* by its shape and position may be regarded as representing one or more supra-dorsal elements belonging to the vertebrae fused with the posterior region of the occipital arch. Thus *Gymnarchus* so far as is known presents the case of a teleost without Weberian apparatus and with a superior occipital cartilage. In Teleostei and lower Teleostomi there are various instances in which vertebral elements become fused behind the occipital arch proper. In these cases, behind the occipital arch, occipitospinal arches (neural arches of fused vertebrae) project as slender processes from the parachordals, but the supradorsals of the fused vertebrae are not differentiated. In *Gymnarchus* on the other hand the supradorsals are represented as the superior occipital cartilage but no differentiated occipitospinal arches are present. The only evidence of vertebral fusion is provided by the multiplicity of the mixed nerves between the occipital arch and the neural arch of the first free vertebra.

The cartilage of the auditory capsule does not show any specialized features. As in all other teleosts the medial wall of the capsule is absent. The division of the cavity of the auditory capsule by a membranous partition, which subsequently becomes ossified, is a secondary adaptation brought about by the inclusion of the distended diverticulum of the air-bladder within the cavity of the capsule. The closure of the basi-capsular fenestra by intramembranous ossification is interesting, since in other Teleosts this fenestra becomes subsequently obliterated by the growth of cartilage bordering it and then ossification follows.

The large development of the cartilage of the side wall of the orbitotemporal region is undoubtedly secondary and unparalleled in any other Teleostei. In this respect *Gymnarchus* has a close resemblance to the lower Teleostomi, especially to *Acipenser*. This, however, does not imply any phylogenetic affinity between the two.

The formation of a pila antotica secundaria in *Gymnarchus*, as reported here for the first time, is of some importance since this structure has not been found in any other teleost hitherto investigated. Typically the side wall of the chondrocranium in front of the foramen for the trigeminal nerve is formed by the pila antotica as exemplified in Selachii, the details of which are well known (de Beer, 1931) and need no description. Considering the lower Teleostomi, the side wall between the trigeminal foramen and the pituitary-vein foramen is present in those forms which lack a posterior myodome. In *Lepidosteus* the cartilage of the side wall in this region is partly in the position of a selachian pila antotica, but it is not typical as it lies a considerable distance in front of the pro-otic bridge, for which reason de Beer (1937) named it pila antotica secundaria. In *Acipenser* the pila antotica is nearer to the selachian form and therefore is called as such. In *Polypterus* the side wall of this region although present, does not answer the requirements of a pila antotica, being posterior to the profundus nerve. Thus it would be seen that the side wall of this region in these fishes shows considerable variation in comparison to typical selachian pila antotica. de Beer (1937) has explained this atypical condition of the side wall of these fishes by assuming that the structure in question is a re-formation in this

region after the loss of a functional posterior myodome. The substance of his views is that the reputed ancestral forms (the Palaeoniscids) possessed a functional posterior myodome, as is certain from Watson's work (1925). During the formation of the myodome in these ancestral forms the external rectus muscle, very likely, would have penetrated through the pituitary-vein foramen. The result of this must have been to disturb and break down the pila antotica. The functional myodome as such was inherited by the Teleostomi from the ancestral forms and was afterwards lost. The pila antotica was subsequently re-formed on more or less typical lines in *Acipenser*, and atypically in *Lepidosteus* (pila antotica secundaria). In *Polypterus* the side wall of this region was re-formed in such a markedly atypical manner having different relations to the profundus nerve that it can no longer be regarded even as pila antotica secundaria. According to de Beer, further support for his assumption is provided by the fact that the internal carotid artery takes an atypical course in *Polypterus*, entering the skull laterally and dorsally to the trabecula. In *Acipenser* also, in early stages the internal carotid artery enters the skull by passing inwards over the trabecula. Moreover, though *Acipenser* has no posterior myodome, the junction of the trabeculo-polar bar with the parachordal is at a much more ventral level than the main parachordal plate and the pro-otic bridge. This condition is characteristic of the Holostei and Teleostei, since, owing to the formation of a posterior myodome in these fishes, the external rectus muscle passes in over the area of the trabeculo-parachordal junction, pressing it down. All these peculiar morphological relationships are explained if it is assumed that these fishes " had possessed a functional myodome (involving a breakdown of the pila antotica and discontinuity of the trabeculae, which would enable the internal carotid arteries to slip upwards), and had subsequently lost it and re-formed the cartilaginous side-wall of the skull " (de Beer, 1937). Regarding those Teleostei which lack a functional posterior myodome —some Siluroids, *Anguilla vulgaris*—de Beer maintains that they, too, have lost it on the same lines as did the lower Teleostomi. Up till now no instance of the re-formation of the side-wall in this region was known among these teleosts, and the comparison with the lower Teleostomi was incomplete. *Gymnarchus* thus provides the first example of a teleost in which, after the loss of a functional posterior myodome, the side-wall in this region has been atypically re-formed as a pila antotica secundaria. Other examples may come to light if different forms of such teleosts are investigated.

It is a well known fact that the nasal capsules in Teleostei are very imperfectly developed in the chondrocranium. *Gymnarchus* shows an extreme case of reduction of cartilage in this direction. The floor, roof, anterior, lateral and posterior walls of the nasal capsule are all wanting. Only the rudimentary lamina orbitonasalis and the broad internasal septum are present between the nasal sacs which are laterally far removed from the septum. Thus the nasal capsules are practically non-existent.

The greatly developed pre-optic root of the orbital cartilage in *Gymnarchus* is comparable with the fully formed similar structure of lower Teleostomi and *Amiurus*, particularly of the latter. According to Hammarberg (1937) in *Lepidosteus*, *Amia*, *Siluroidea* and *Clupea* the part (his processus ent-ethmoideus) of the pre-optic root of orbital cartilage opposite the lamina orbitonasalis (his processus ect-ethmoideus) chondrifies independently of the rest of the posterior portion of the pre-optic root. The presence of a pre-optic fontanelle in the pre-optic root of *Gymnarchus* and *Amiurus* can be explained if it is supposed that the two separately chondrifying cartilages, which eventually meet above and below the pre-optic fontanelle to form the pre-optic root, fail to grow in the area which is left as the fontanelle. The pre-optic fontanelle is of no morphological importance. It is covered by a membrane.

The development of the internasal septum in *Amiurus* is interesting. Kindred (1919) describes the anterior boundary of the cranial cavity in a 10 mm. larva as limited by a transverse plate of cartilage, the lamina pre-cerebralis as it is called by de Beer (1937). In later stages a massive internasal septum grows from this lamina

pre-cerebralis. Probably the formation of the septum takes place on similar lines in *Gymnarchus*.

It is in the disposition of the facial nerves that *Gymnarchus* shows the most unusual features. In all fishes hitherto investigated, the mandibular facial and the hyoidean facial nerves arise from the geniculate ganglion by a common trunk with which the root of the palatine nerve may be more or less associated within the skull. But the exit of the palatine nerve from the skull is always without exception distinct and separate from that of the common trunk of the hyomandibular nerve A character that is common among the various groups of fishes is that the hyoidean and mandibular portions of the facial nerve always leave the skull as a common trunk, irrespective of subsequent differences in the relations of the common truncus hyomandibularis and its main branches– the rami hyoideus facialis, mandibularis internus facialis—with the neighbouring muscles during their course and the hyoid arch elements In fact this character is common to all gnathostomes since the homologue of the n. mandibularis internus, the chorda tympani, is always associated with the mandibular facial nerve in its early course and leaves the skull with it. In *Gymnarchus*, as is evident from the foregoing description, the two nerves of this complex are quite independent, they arise within the skull from the geniculate ganglion separately and pass out from the skull by separate foramina. The ramus mandibularis facialis runs external to the quadrate, and in its entire course is considerably anterior to the hyomandibula. The ramus hyoideus facialis, on the other hand, comes out through a separate foramen in the pro-otic bone (=foramen externum hyoideum in the jugular canal), medio-ventral to the hyomandibular articulation. In its subsequent course the relations of the hyoidean nerve to the adductor muscle of the mandible and hyomandibular cartilage are exactly the same as that of the common hyomandibular trunk of other generalized teleosts. In between the origin of these two nerves from the geniculate ganglion are interpolated the n. opercularis superficialis facialis the n. dorsalis cutaneus facialis and the palatine nerves and the n. pre-trematicus facialis Except the n. opercularis superficialis facialis all these nerves arise from the geniculate ganglion independently. The n. opercularis superficialis is only partially associated with the roots of the nn. dorsalis cutaneus facialis et mandibularis facialis, and therefore can be regarded almost as a separate nerve. In the accompanying table (p. 478) an attempt is made to compare the branches of the facial nerve of *Gymnarchus* with those of *Menidia*. The cranial nerves of the latter fish are best known among the teleostean fishes as a result of an exhaustive study by Herrick (1899). The table only gives a generalized idea of the main differences between these two fishes, as in the absence of a detailed study of the nerves of *Gymnarchus* it is not possible to do otherwise.

The n. dorsalis cutaneous facialis is to be regarded as a new development from the facial nerve. So far as I know one cannot compare it with any branch of the facial nerve of any other fish. It appears to be an extra nerve chiefly developed for the innervation of the so-called multicellular glandular organs of the skin of *Gymnarchus*. Pehrson (1945) in his paper on the larval pit organ lines of *Gymnarchus niloticus* mentions : " The skin of *Gymnarchus* is unusually thick and lacks scales, but on the other hand, it is supplied with densely lying glandular organs, innervated from the trigeminus." I do not agree with his observation. My study shows that the chief innervation of these glands is from the facial nerve—not only through the especially developed n. dorsalis cutaneus facialis but also through the nn. opercularis superficialis et mandibularis facialis. I have, however, not followed the innervation of all these glands in the entire larva. Possibly there may be some areas innervated by any branch from the trigeminal system, but if there are any, they would be insignificant indeed in comparison to the share of the facial nerve.

TABLE OF COMPARISON OF THE FACIAL NERVES OF *MENIDIA* AND *GYMNARCHUS*.

MENIDIA (Herrick, 1899).			GYMNARCHUS.		
No. of independent nerves arising from the geniculate ganglion.	No. of important branches of these nerves.	Name of nerves and their branches.	No. of independent nerves arising from the geniculate ganglion.	No. of important branches of these nerves.	Name of nerves and their branches.
1.		*Ophthalmicus superficialis*, VII.	1.		*Ophthalmicus superficialis*, VII.
2.		*Oticus.*	2.		*Oticus.*
3.		*Buccalis.*	3.		*Buccalis.*
4.		*Palatinus.*	4.		*Palatinus.*
5.		*Pretrematicus facialis.*	5.		*Pretrematicus facialis.*
6.		*Truncus hyomandibularis.*	6.		*Nervus hyoideus.*
	1.	Ramus hyoideus.		1.	Ramus operecularis profundus facialis.
	2.	Ramus operecularis profundus facialis.	7.		*Nervus operecularis superficialis facialis.*
	3.	Ramus operecularis superficialis facialis.	8.		*Nervus mandibularis facialis.*
	4.	Ramus mandibularis.			
		(*a*) mandibularis externus.		1.	Ramus mandibularis externus.
		(*b*) mandibularis internus.		2.	Ramus mandibularis internus.
			9.		*Nervus dorsalis cutaneous facialis.*
				1.	Ventral ramus. Anterior ramus.
				3.	Posterior ramus.

It has been shown in this paper that larval *Gymnarchus* lacks basal and basitrabecular processes and that Assheton's figure showing these processes is erroneous. The jaw suspension is methiostylic in the larval stage. In this respect, therefore, it does not differ from other Teleostei. The relation of the n internus mandibularis facialis to the quadrate is peculiar in *Gymnarchus*. This nerve as it branches from the n. mandibularis facialis laterally to the quadrate, enters a foramen in the quadrate and then runs medially to it and Meckel's cartilage. In other teleosts this nerve in its postero-anterior course passes laterally to the symplectic, if this cartilage is present either separate or fused with the hyomandibula, and then runs medially to the lower portion of the quadrate and from thereon medially to Meckel's cartilage. No foramen is formed in the quadrate for this nerve.

The relations of the glossopharyngeal nerve to the ear in *Gymnarchus* as described in the foregoing are easily explicable. de Beer (1931) has shown that originally the glossopharyngeal nerve comes out together with the vagus through the fissura

metotica behind the auditory capsule. The inclusion of the glossopharyngeal nerve within the cavity of the auditory capsule in the majority of teleosts, where the nerve traverses the basi-capsular fenestra, is secondary and indicates that a portion of the fissura metotica has been included in the basi-capsular fenestra. This condition is found in larval *Salmo* (de Beer, 1927, 1931). *Gymnarchus* resembles *Salmo* in this respect. In spite of the topographical change in the course of the glossopharyngeal nerve within the auditory capsule, the morphological relations of this nerve to the ear are essentially the same as in *Salmo*. (Compare fig. 19 with de Beer's fig. 43, p. 301 (1927)). In *Salmo* the glossopharyngeal nerve runs between the sacculus and the utriculus posteriorly to the sacculo-utricular junction. If the sacculus of *Salmo* were to swing from its ventro-medial position to a lateral position in relation to the utriculus, and at the same time the sacculo-utricular junction were to be produced into a long and thin canalis reuniens, then the glossopharyngeal nerve would pass ventrally to the utriculus and would run between the utriculus and the sacculus posteriorly to the canalis reuniens. This is the condition as found in *Gymnarchus*.

4. Summary.

The chondrocranium of two larval stages of *Gymnarchus niloticus*—one 15-day old, the other of an unknown but of slightly younger stage—have been studied. The morphological relations of the arteries, veins and nerves of the head have been described in detail, and the results have necessitated a rectification of some of the statements made by Assheton. The cartilage of the chondrocranium is greatly developed but conform to the general Teleostean type with certain peculiarities of its own. The larval skull is platytrabic. The auditory capsule is greatly developed and contains a modified ear and a sac-like extension of the air-bladder. The internal cavity of the capsule is divided by a partition which is partly ossified. In the lateral wall of the capsule is a vacuity covered by a membrane lateral to which extends the expanded portion of the temporal and supratemporal latero-sensory canals. There is an extensively developed orbital cartilage with pre-optic and metoptic roots and a pila antotica secundaria. The anterior and posterior myodomes are absent. All the eye muscles are collected in a fibrous orbital capsule. The internal carotid foramen is separated from the hypophyseal fenestra. There is no pro-otic bridge. There is a well-developed trigemino-facialis chamber. A lateral commissure is present. Nasal capsules are practically absent except for a broad and massive internasal septum and a rudimentary lamina orbitonasalis. The pterygoquadrate is in a pro-cartilagenous fusion with the hyomandibula. Neither otic, nor basal, nor basi-trabecular articulations are present. The larval jaw suspension is methyostylic.

Unique features in *Gymnarchus* not present in any known living teleost are: (1) presence of a pila antotica secundaria, (2) splitting of the common truncus hyomandibularis of other fishes into more or less three separately originating nerves—n. mandibularis, n. opercularis superficialis, and n. hyoideus, (3) formation of an extra nerve, the dorsalis cutaneus facialis, in the facialis system.

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6. EXPLANATION OF LETTERING.

In n. olfactorius ; *IIn* n. opticus ; *IIIn* n. oculomotorius ; *IVn* n. trochlearis ; *Vmand* n. mandibularis trigeminus ; *Vmax* n. maxillaris trigeminus ; *Voph* n. ophthalmicus superficialis trigeminus ; *VIn* n. abducens ; *VIIbuc* n. buccalis facialis ; *VIIdors.cutn.* or *VIIdcmt* n. dorsalis cutaneus facialis, main trunk ; *VIIdors.cutn.ab* or *VIIdcab* n. dorsalis cutaneus facialis, anterior branch ; *VIIdors.cutn.pb* or *VIIdcpb* n. dorsalis cutaneus facialis, posterior branch ; *VIIdors.cutn.vb* or *VIIdcvb* n. dorsalis cutaneus facialis, ventral branch ; *VIIhyoid* n. hyoideus facialis ; *VIImand* n. mandibularis facialis ; *VIIoperc.super.* or *VIIos* n. opercularis superficialis facialis ; *VIIoperc.prof.* or *VIIopf* n. opercularis profundus facialis ; *VIIoph* n. ophthalmicus superficialis facialis ; *VIIot* n. oticus facialis ; *VIIpn* n. palatinus facialis ; *VIIIn* n. acusticus ; *IXn* n. glossopharyngeus ; *Xn* n. vagus.

aa ampulla of anterior semicircular canal ; *aart* anterior artery ; *abc* anterior basicapsular commissure ; *abdc* anterior branch of n. dorsalis cutaneus facialis ; *ac* auditory capsule ; *acr* arteria centralis retinae ; *acv* anterior cerebral vein ; *acvf* anterior cerebral vein foramen ; *ahm* musculus adductor hyomandibularis ; *alc* ampulla of lateral semicircular canal ; *alf* antero-lateral fontanella ; *alv* anterior lateral vein ; *aom* arteria ophthalmica magna ; *apc* ampulla of posterior semicircular canal ; *asc* anterior semicircular canal ;

b bone ; *bcf* basicapsular fenestra ; *bdlc* blind diverticulum of the latero-sensory canal (=blind primary pore-tube) ; *bob* basioccipital bone ; *bVIIbuc* branch of n. buccalis facialis ; *br* brain ; *bsr* branchiostegal ray(s) ;

ca carotid artery ; *cdab* cylindrical diverticulum of the air-bladder ; *ch* ceratohyal ; *cp* crista parotica ; *cr* canalis reuniens (between utriculus and sacculus) ;

del ductus endolymphaticus ; *dm* dura mater ; *dpd* dermopalatine bone ;

e eye ; ebv_{1-4} efferent branchial vessels 1 to 4 ; *embVII* external mandibular branch of n. mandibularis facialis ; *epb* epiphysial bar ; *epl* ethmoid plate ;

fIII and *IVn* common foramen for oculomotor and trochlear nerves ; *fb* frontal bone ; *feh* foramen externum hyoidei ; *fg* facial or geniculate ganglion ; *fh* foramen in hyomandibula for n. hyoideus facialis ; *fin* foramen in quadrate for n. mandibularis facialis internus ;

gahm groove for the articulation of hyomandibula ; *gln* n. glossopharyngeus ; *glnstb* supratemporal branch of the glossopharyngeal nerve ;

hdv head vein ; *hf* hypophyseal fenestra ; *hic* horizontal infraorbital latero-sensory canal ; *hmb* hyomandibular bone ; *hmc* hyomandibular cartilage ;

ica internal carotid artery ; *icf* foramen for internal carotid artery ; *ila* inner lateral aorta ; *imbVII* internal mandibular branch of n. mandibularis facialis ; *imehb* intramembranous extension of hyomandibular bone ; *imepob* intramembranous extension of pro-otic bone ; *ins* internasal septum ; *iopb* interopercular bone ; *iov* inferior orbital vein ; *itb* intertemporal bone ;

jc jugular canal ; *jf* jugular or metotic foramen ;

lav lateral auditory vacuity ; *lg* lagena ; *lon* lamina orbitonasalis ; *lsc* lateral semicircular canal ;

m_1 membrane covering the lateral auditory vacuity ; m_2 membranous partition between utriculus and sacculus ; *mc* Meckel's cartilage ; *mdc* mandibular latero-sensory canal ; *mor* metoptic root of orbital cartilage ; *mp* membranous partition between utriculus and sacculus ; *mtb* metapterygoid bone ; *mxb* maxillary bone ;

na nasal artery ; *nb* nasal bone ; *nc* notochord ; *ns* nasal sac ;

oa occipital arch ; *oc* orbital cartilage ; *ocp* orbital capsule (enclosing the eye and eye muscles) ; *ocrs* opening of canalis reuniens in sacculus ; *ocru* opening of canalis reuniens in utriculus ; *of* olfactory foramen ; *ola* outer lateral aorta ; *oma* orbitobasal artery ; *opa* opercular artery ; *opf* optic foramen ;

pab paraphysal bar ; *pas* pila antotica secundaria ; *pb* parietal bone ; *pbaa* posterior branch of anterior artery ; *pbc* posterior basi-capsular commissure ; *pbdc* posterior branch of n. dorsalis cutaneus facialis ; *pc* parachordal ; *pfb* postfrontal bone ; *pg* pars ganglionaris ; *pj* pars jugularis ; *pmo* pila metoptica ; *pmx* premaxillary bone ; *pma* palatine artery ; *pob* pro-otic bone ; *pobb* postorbital bone ; *pof* pro-otic foramen ; *polc* preopercular latero-sensory canal ; *pop* pro-otic process ; *popb* preopercular bone ; *poptf* preoptic fontanelle ; *por* postorbital root of orbital cartilage ; *poroc* preoptic root of orbital cartilage ; *ppp* post palatine process ; *ppl* parachordal plate ; *pq* pterygoquadrate ; *psb* parasphenoid bone ; *ptp* pterygoid process of quadrate ; *pv* pituitary vein ; *pvb* prevomer bone ; *pvf* pituitary vein foramen ;

qb quadrate bone ; *qu* quadrate ;

rglv root of glossopharyngeal nerve ; *rtv* root of trigeminal nerve.

s sacculus ; *sbob* suborbital bone ; *sbolc* suborbital latero-sensory canal ; *sc* strip of cartilage (part of pre-optic root) between olfactory foramen and pre-optic fontanelle ; *sdab* sac-like diverticulum of the air-bladder ; *seb* supra-ethmoid bone ; *slc* sacculo-lagenar canal ; *soc* superior occipital cartilage ; *sov* superior orbital vein ; *sphb* sphenotic bone ; *spolc* supraorbital lateral line canal ; *spq* space in pterygoquadrate covered by intramembranous bone ; *ssu* septum semicirculare anterius ; *ssl* septum semicirculare laterale ; *ssp* septum semicirculare posterius ; *stb* supratemporal bone ; *stsd* supratemporal sensory diverticulum ;

tc trabecula cranii ; *tcom* trabecula communis ; *tg* trigeminal ganglion ; *ts* tectum synoticum ; *ttm* taenia tecti medialis ; *ttma* taenia tecti medialis anterior ;

ut utriculus ; *vrc* vertical ridge of cartilage.

The Anterior Brain-case and Interorbital Septum of Sauropsida, with a consideration of the Origin of Snakes.

By A. d'A. BELLAIRS, Department of Anatomy, London Hospital Medical College.

(PLATES 9–11, and 9 Text-figures.)

[Read 22 January 1948]

INTRODUCTION.

The anterior part of the brain-case in all vertebrates consists of a more or less complete casing of cartilage or bone surrounding the central nervous system. It separates the latter from the pharynx and respiratory apparatus below, and gives origin to the eye muscles. Its walls are pierced by foramina for the nerves and vessels of the orbital region. Its shape in any species is associated with the sizes and positions of the organs in the vicinity.

The anterior brain-case may be described as that part of the skull which lies between the posterior wall of the nasal capsule in front, and the basal plate and otic capsule behind. In all tetrapods it includes both membrane bone and endocranial components; the latter correspond with the orbito-temporal part of the chondrocranium in the embryo. During the course of ontogeny the endocranial skeleton in this region is developed from two morphologically distinct elements: the orbital cartilages and their extensions above, and the trabeculae below. The former develop in relation to an ectomeningeal condensation surrounding the brain, while the latter are regarded as primitively extra-cranial structures, probably representing the cartilages of a vanished branchial arch, which have become secondarily incorporated into the brain-case (for discussion see de Beer, 1937). The trabeculae and orbital cartilages are closely associated throughout ontogeny in most forms, but the trabeculae differ from the latter in that they contribute not only to the brain-case, but also to the nasal capsule.

In the fully developed chondrocranium the trabeculae are characteristically fused at their anterior ends, giving rise to midline nasal septum elements. Their posterior ends are always divergent, fusing with the parachordals and polar cartilages (when present) and enclosing the hypophyseal fenestra. They show considerable variations, however, in their relations to one another in the orbital region. In those forms where they are separated at this level (e.g. urodeles, fig. 1A: snakes, fig. 1E, etc.) the chondrocranium is said to be platytrabic (Van Wijhe, 1922) or platybasic (Gaupp, 1900); in other forms (e.g. lizards, figs. 2–4, etc.), in which the trabeculae are fused together to form a trabecula communis, the condition is described as tropitrabic (or tropibasic). There is no absolute distinction between these two types, since many, if not all non-mammalian chondrocrania are initially platytrabic, but some become tropitrabic later in ontogeny.

In tropitrabic forms the trabeculae are fused behind the ethmoidal region and often form, usually with the help of other elements, an interorbital septum. This is a median plate of cartilage or bone which may become secondarily fenestrated during development, the vacuities remaining occupied by membrane. The interorbital septum is bounded posteriorly by the optic foramina, behind which the trabeculae diverge, and is continuous in front with the nasal septum. In characteristically tropitrabic forms such as lizards (fig. 1C, etc.) and crocodiles (fig. 5B) the médial borders of the orbital cartilages are also approximated to the midline and become inflected vertically downwards, fusing with the underlying trabecula communis and forming the upper part of the interorbital septum. In such forms, therefore, the trabeculae do not enter into the floor of the cranial cavity.

The upper parts of the orbital cartilages lie in a more horizontal plane, and in the middle and posterior orbital regions they form two laterally directed wings which together constitute the planum supraseptale. Behind the optic foramina both orbital cartilages and trabeculae retain their paired nature, the junction between the two being represented by the pila metoptica. Only those parts of the trabeculae and orbital cartilages which lie anterior to the optic foramina, therefore, contribute to

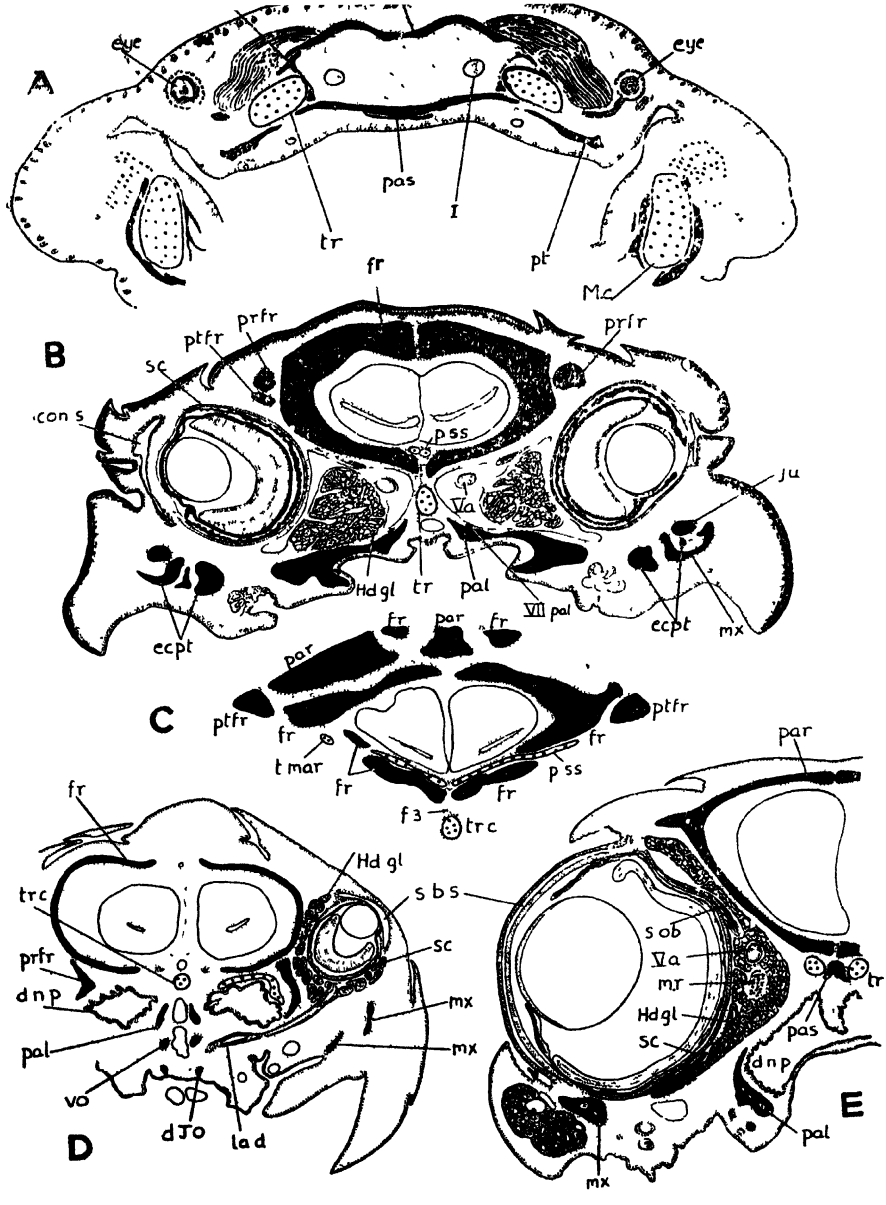


FIG. 1.- Transverse sections through mid-orbital region of head in an amphibian and four squamate types, showing disposition of platytrabic and tropitrabic chondrocrania.

A. *Proteus anguinus*, adult (platytrabic). The eyes are highly degenerate in this cave-dwelling salamander. (× 13.)

B. *Anniella pulchra*, subadult (tropitrabic). The eyes are reduced in this burrowing limbless lizard, but a low interorbital septum is present. (× 30.)

C. *Anniella*. Transverse section through brain-case slightly posterior to level of B, showing maximum extent of planum supraseptale, and its relationship to frontal downgrowths. (× 30.)

D. *Typhlops diardi*, late embryo (modified platytrabic). Owing to reduction of the eyes and telescoping of front part of head, the trabecula communis, and not the paired trabeculae, lies at mid-orbital level in this specialized burrowing snake. (× 26.)

E. *Bungarus fasciatus*, subadult (platytrabic). The usual ophidian disposition of the trabeculae is present in this large-eyed snake. (× 13.)

the formation of the interorbital septum. The essential patterns of the tropitrabic and platytrabic chondrocrania, and their relationship to the orbits and brain are illustrated in cross-section in fig. 1.

In many types the chondrocranium in the orbitotemporal region is partly or wholly replaced by bone ; the trabeculae ossify to form the presphenoid and the anterior part of the basisphenoid, while the orbital cartilages give rise to the orbitosphenoids, and further back to the laterosphenoids (or pleurosphenoids), which ossify in the pila antotica. In most modern reptiles, however, these replacement ossifications are small or absent ; all or most of the anterior brain-case, together with the nasal capsule, remains cartilaginous throughout life. A more rigid framework is supplied, however, by membrane bones such as the frontals and parietals above and the parasphenoid below, which are closely associated with the cartilaginous brain-case in most forms.

The following account deals with the condition of the anterior brain-case, with special reference to the trabeculae and orbital cartilages. For present purposes the latter may be regarded as comprising all the paired lateral elements of this part of the endocranial brain-case, from the sphenethmoid commissures in front to the pila antotica behind. The hypophyseal region in *Sphenodon* and lizards has recently been described by Säve-Södebergh (1946), and will not be considered in detail here.

A brief review of the morphology of the anterior brain-case is given below, and this part of the skull in reptiles is then described in greater detail. Owing to the lack of ossification in this region, paleontological data are necessarily incomplete, and knowledge of its morphology must be largely based on living forms. The distribution of the interorbital septum among different groups is especially considered, and the embryology of this structure in certain species is also described. Certain observations on the avian brain-case have also been included, since this may be regarded as a specialized derivative of the archosaurian type.

Material and Methods.

The original data recorded below have been largely based on an extensive collection of sectioned reptile heads which includes a number of hitherto undescribed forms ; a list of all genera examined is given at the end of this paper. I am indebted to the following who have kindly provided opportunities for discussing my observations, and for the examination and acquisition of material : Dr. C. M. Bogert, Dr. P. M. Butler, Prof. G. R. de Beer, Mr. A. Fisk, Prof. F. Goldby, Dr. R. S. Hawes, Mr. W. Warwick James, Mr. J. Lester, Dr. R. E. Rewell and the Zoological Society of London, Mr. A. Loveridge, Prof. D. Mackinnon, Dr. L. Harrison Matthews, Mr. C. M. Miller, Dr. J. A. Oliver, Mr. H. W. Parker, Mr. F. R. Parrington, Mr. C. W. M. Pratt, Dr. Malcolm Smith, Dr. W. E. Swinton, Prof. D. M. S. Watson. I am also indebted to Mr. R. Quinton Cox and Mr. A. J. King for technical assistance.

The Anterior Brain-Case throughout the Tetrapod Series.

The work of Watson (1926), Romer (1937), Jarvik (1942) and others has shown that in the osteolepid crossopterygians the anterior brain-case, together with much of the nasal capsule, was ossified to form the ethmosphenoid bone. This formed a complete investment for the olfactory nerves and forebrain and presumably included ossifications of the trabeculae and orbital cartilages. Romer (1937), describing conditions in *Megalichthys*, suggests that in the embryo the trabeculae must have lain quite close together and ' The condition would thus have been an intermediate one from which either a platybasic or a tropibasic condition might have been derived '.

In the early embolomerous labrinthodonts conditions appear to have resembled those in osteolepids (Watson, 1926 ; Romer, 1937, 1947). In the amphibia, however, the nasal capsule was cartilaginous and the bony brain-case (the anterior part of which is termed the sphenethmoid) was not divided into two segments by an unossified zone, a characteristic crossopterygian feature (see Westoll, 1933). In the interorbital region the brain-case was higher and narrower in the embolomer than in the fish, and the chondrocranium was apparently of the tropitrabic type.

In many later labyrinthodonts the brain-case became flattened and the interorbital septum disappeared, the chondrocranium apparently becoming platytrabic. At the same time the ossifications of the skull and body skeleton were reduced. Such changes occurred independently in many groups and were probably associated with the assumption of completely aquatic and sluggish habits. These conditions are suggestive of neoteny and are comparable with those which have occurred in perennibranchiate urodeles such as *Proteus* (fig. 1 A). In all groups of modern amphibia the chondrocranium is markedly platytrabic and the sphenethmoid ossification has been more or less reduced.

The most primitive reptiles appear to have inherited the tropitrabic type of brain-case which was present in the early labyrinthodonts. Some reduction in the extent of ossification had taken place, however, especially on the dorsal aspect, where the frontals and parietals provided a new roof for the cranial cavity (see Romer, 1946, on *Limnoscelis*: Olson, 1947, on *Diadectes*).

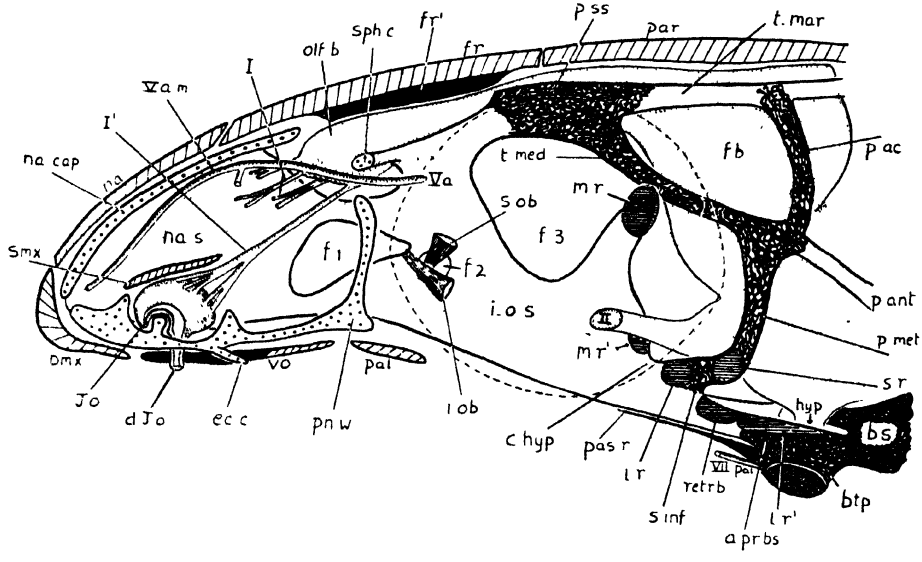


FIG. 2.—Diagrammatic reconstruction of bones, cartilages and related structures of the anterior brain-case of a lizard seen in lateral view, with the nasal capsule in paramedian section (partly based on *Lacerta*). Membrane bones shown in black, cut bone surfaces shown by slanting lines; parts of chondrocranium liable to ossify shown in white stipple on black. Attachments of eye muscles based on account by Pearson (1921) for *Lygosoma*. Outline of orbit shown in interrupted lines.

In the pelycosaurs such as *Dimetrodon* (Romer and Price, 1940) and many therapsids (see Olson, 1944) the anterior brain-case was ossified and a well developed interorbital septum was present. Distinct presphenoid and orbitosphenoid elements are distinguished by Olson in the sphenethmoid complex of gorgonopsians, foreshadowing conditions in mammals. During the course of mammalian evolution a number of changes in the configuration of the anterior brain-case occurred, including the loss of the interorbital septum. It is hoped that an account of this region of the skull in mammals will be given in a later paper, with special reference to the redevelopment of the interorbital septum in a number of mammalian groups.*

* This work was originally begun in conjunction with Prof. R. Wheeler Haines, and was intended to cover both Sauropsida and Mammalia. Owing to Prof. Haines' departure to Egypt, however, it has not been possible to continue the collaboration. It was decided, therefore, that the Sauropsida and Mammalia should be dealt with separately, and that conditions in the latter group should be described by Prof. Haines.

The scanty paleontological evidence available, together with conditions described later in *Sphenodon*, the most primitive of modern reptiles, suggests that (except in those forms on the mammalian line of evolution) the ossifications in the anterior brain-case had become markedly reduced at an early period in reptilian history, while the chondrocranium remained characteristically tropitrabic, with a high interorbital septum. From a brain-case of this type it is thought that the conditions present in more specialized reptiles and birds have been derived.

Conditions in Sauropsida.

1. *Sauria, Rhynchocephalia, Testudines and Crocodilia : adult morphology.*

Since Gaupp's account of *Lacerta agilis* (1900) numerous workers have studied the reptilian chondrocranium in representatives of all groups. In general, conditions in Sauria are best known ; this has somewhat obscured the fact that this group presents a number of specialized features, in particular the reduction of the endocranial brain-case in the orbito-temporal region, which are not characteristic of the more conservative forms such as turtles and crocodiles. Nevertheless, conditions in lizards are readily comparable with those in other reptiles, and the following account is applicable to living reptiles in general, except for the snakes and amphisbaenids, which will be treated separately.

The anterior endocranial brain-case is largely cartilaginous. In the orbital region its floor and side-walls are represented only by the sphenethmoid commissures, the two wings of the planum supraseptale and its posterior extensions which connect it with the basal plate, and the interorbital septum (figs. 2–4, etc.). The small ossifications which may occur in this region are best described in relation to the chondrocranium.

The sphenethmoid commissures represent the anterior parts of the lateral walls of the brain-case, and run from the roof of the nasal capsule in front to the apex of the planum supraseptale behind (figs. 2–4, etc.). They support the ends of the olfactory bulbs, which project over them into the fenestra olfactoria. In some forms, (e.g. *Calotes*, Ramaswami, 1946 : *Nessia*, *Varanus*, figs. 3, 4) they fuse completely with each other and with the underlying interorbital septum to form the pre-optic pillar, before the brain-case widens out behind as the wings of the planum supraseptale. In adult specimens of *Lialis* the sphenethmoid commissures appear to be absent.

The planum itself constitutes the most extensively developed part of the endocranial brain-case in the orbito-temporal region. It consists of two expanded wings, partly fused with each other and with the interorbital septum below, which run to a point anteriorly. The trough so formed supports the olfactory bulbs and lies above the orbits (figs. 2, 3). The extent of the planum is much reduced in lizards, where the posterior border is encroached on by large fenestrae.

Behind the planum supraseptale the walls and floor of the brain-case are fenestrated, being continued backwards as a series of cartilaginous bars which join the basal plate and otic capsule. These develop as distinct elements, and have received separate names (taeniae marginales, taeniae mediales, pila metoptica, pila antotica, etc : see figs. 2–6, etc), but it may be emphasized that they merely represent the persistent portions of the more extensive tubular brain-case found in primitive tetrapods. The extent and disposition of these bars, together with the fenestrae which they enclose, have been very thoroughly described by Gaupp (1900, 1906) and de Beer (1937) in *Lacerta*, but differ considerably among the various reptilian groups.

In *Sphenodon* (Howes and Swinnerton, 1900) and lizards the fenestrae are characteristically large and the bars which surround them are slender and often incomplete. In most lizards (e.g. *Anguis*, Zimmerman, 1913, and fig. 6A : *Acontias*, Brock, 1941 : *Nessia* : *Anniella*, fig. 1B, C : *Lialis*, fig. 9K–M : *Varanus*, figs. 3, 4) the reduction of cartilage has proceeded even further than in *Lacerta* (see fig. 2), foreshadowing the condition in snakes. The taeniae marginales and pila metoptica, which form the posterior boundaries of the optic foramina, appear to be the most constant of these bars ; in some cases (e.g. *Eumeces*, Rice, 1920) some of the

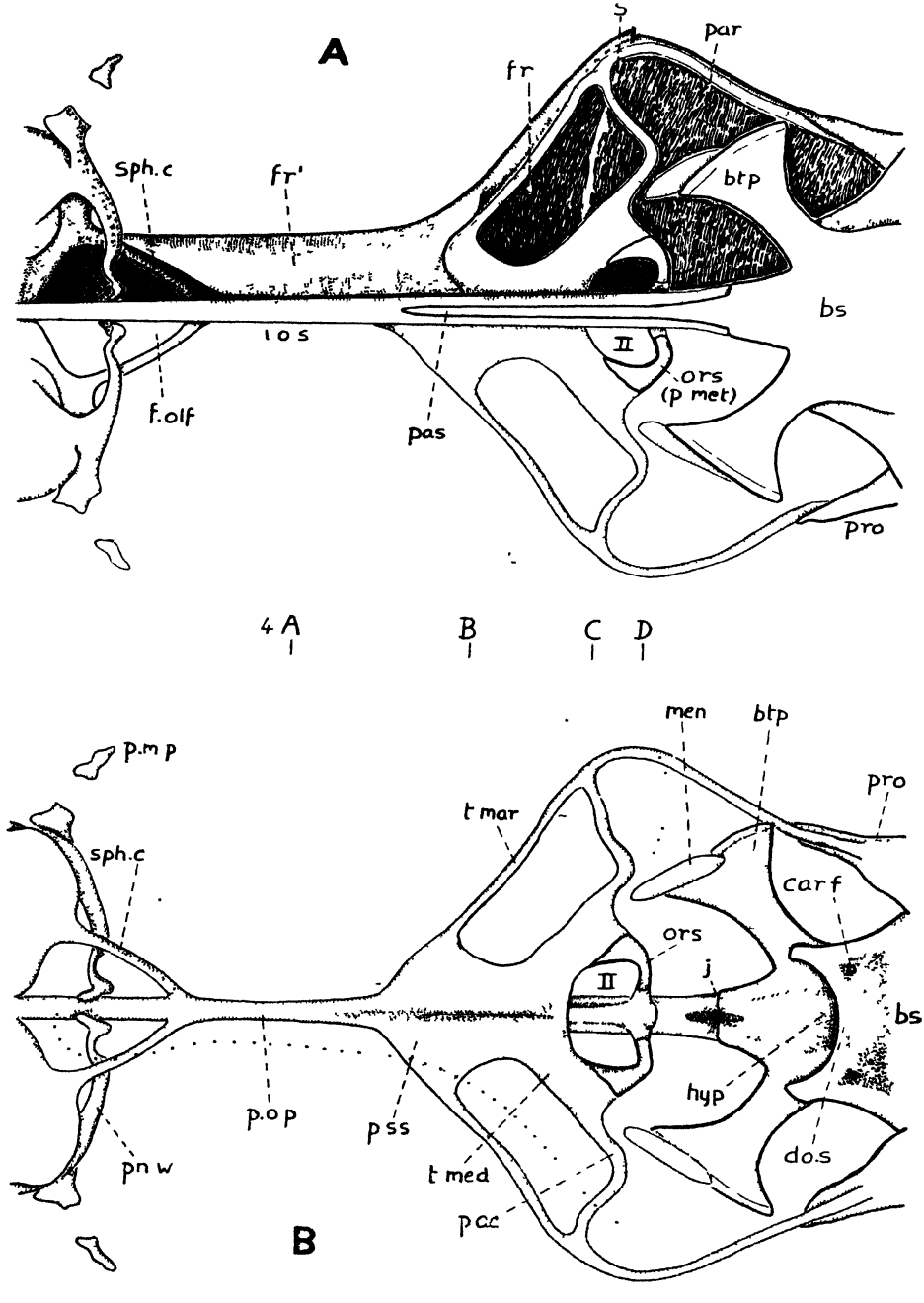


FIG. 3.—Anterior endocranial brain-case of *Varanus monitor* (subadult), partly based on a graphic reconstruction. The ossified parts are drawn in thick outline. Levels of section in fig. 4 are shown. (×10.)

A. Ventral view. Extent of frontal downgrowth shown on one side.
B. Dorsal view. Outline of brain on left, and orbit on right side are dotted.
j, junction between trabecula communis and basisphenoid ossification.
s, fronto-parietal suture.

cartilages in this region undergo retrogression during the later stages of embryonic life. In Testudines (fig. 6B and Pl. 11) and Crocodilia (fig. 5B, C) these cartilages are more massively developed and the foramina are correspondingly less extensive.

This reduction and fenestration of the lateral walls of the brain-case has given rise to the state in many reptiles where large areas of the cranial cavity are bounded only by membrane. Some compensation may be provided, however, by downgrowths from the roofing membrane bones which take on the function of the primitive sphenethmoid ossification. The distribution and extent of these downgrowths is very variable. In *Sphenodon*, agamid and lacertid lizards and Crocodilia, for instance, they are absent altogether, or only form slight ridges on the lower aspect of the cranial roof. Among the forms examined by us, downgrowths from the frontals encircling the olfactory bulbs were found in some turtles (e.g. *Chelydra*) and many lizards : Varanidae (figs. 3, 4), Geckonidae, Pygopodidae (fig. 9K–M), some skinks (*Acontias*, Brock, 1941 ; *Nessia*), Anniellidae. Downgrowths from the parietals have been reported by Brock in *Acontias*, and are also present in turtles, where they join the pterygoids below. This grouping appears to have little phylogenetic significance, and is also difficult to explain on adaptive grounds (see later). Whereas turtles, varanids and geckos exhibit no burrowing adaptations, the other lizards cited are all more or less specialized for burrowing life.

The relationship of the frontal downgrowths to the endocranial brain-case is variable. In Crocodilia (fig. 5B) they only cover the lateral aspects of the olfactory bulbs and lie entirely dorsal to the planum supraseptale. In many lizards (.e.g *Varanus*, figs. 3, 4) they completely surround the anterior parts of the olfactory bulbs but diverge posteriorly, leaving a gap in the midline into which projects the apex of the planum supraseptale. In geckos and in the pygopodid *Lialis* the two frontal downgrowths are completely fused over the greater part of their extent, so that the anterior part of the planum supraseptale is completely excluded from the cranial cavity (fig. 9K–M). In *Anniella* (fig. 1A, B) the wings of the planum pass through notches on the posterior borders of the frontal downgrowths, so that in cross section they appear to perforate the bone.

An interorbital septum has been found in all living reptiles where the chondrocranium is known, except for the snakes and amphisbaenids described later. Camp (1923) states that this structure is absent in Anniellidae, but examination of microscopic sections indicates that a low septum is present. Its occurrence has still to be confirmed, however, in certain other families of burrowing lizards such as the Dibamidae and Anelytropsidae.

The adult morphology of the interorbital septum is relatively constant. It is continuous anteriorly with the nasal septum, and posteriorly it ends at the level of the optic foramina, where its lower part is continuous with the trabecula communis (fig. 2). In Testudines and Crocodilia the pila metoptica join the trabecula communis directly behind the optic foramina, just anterior to the level at which it forks into the paired trabeculae. In *Sphenodon* and lizards, however, the pila metoptica join to form a flattened plate, the subiculum infundibuli, which is continued forwards above the trabecula communis as a separate narrow rod, the cartilago hypochiasmata, which joins the posterior vertical border of the interorbital septum (fig. 2).

In many reptiles the interorbital septum contains a number of vacuities filled with membrane, and these are particularly extensive in *Sphenodon* and lizards. Their distribution is variable, but in general conforms to a certain pattern (fig. 2). The most anterior (fenestra 1) is situated in the transitional region between the nasal and interorbital parts of the septum. In some lizards (e.g. *Anguis*, *Hemidactylus*, *Varanus*) the upper bar enclosing this fenestra is absent and the septum in this region is consequently low. A little further back is a small and inconstant fen. 2 (absent in geckos), and above and behind this is the very large fen. 3 which forms a gap between the trabecular part of the septum and the planum supraseptale. These vacuities are small or absent in Testudines and Crocodilia.

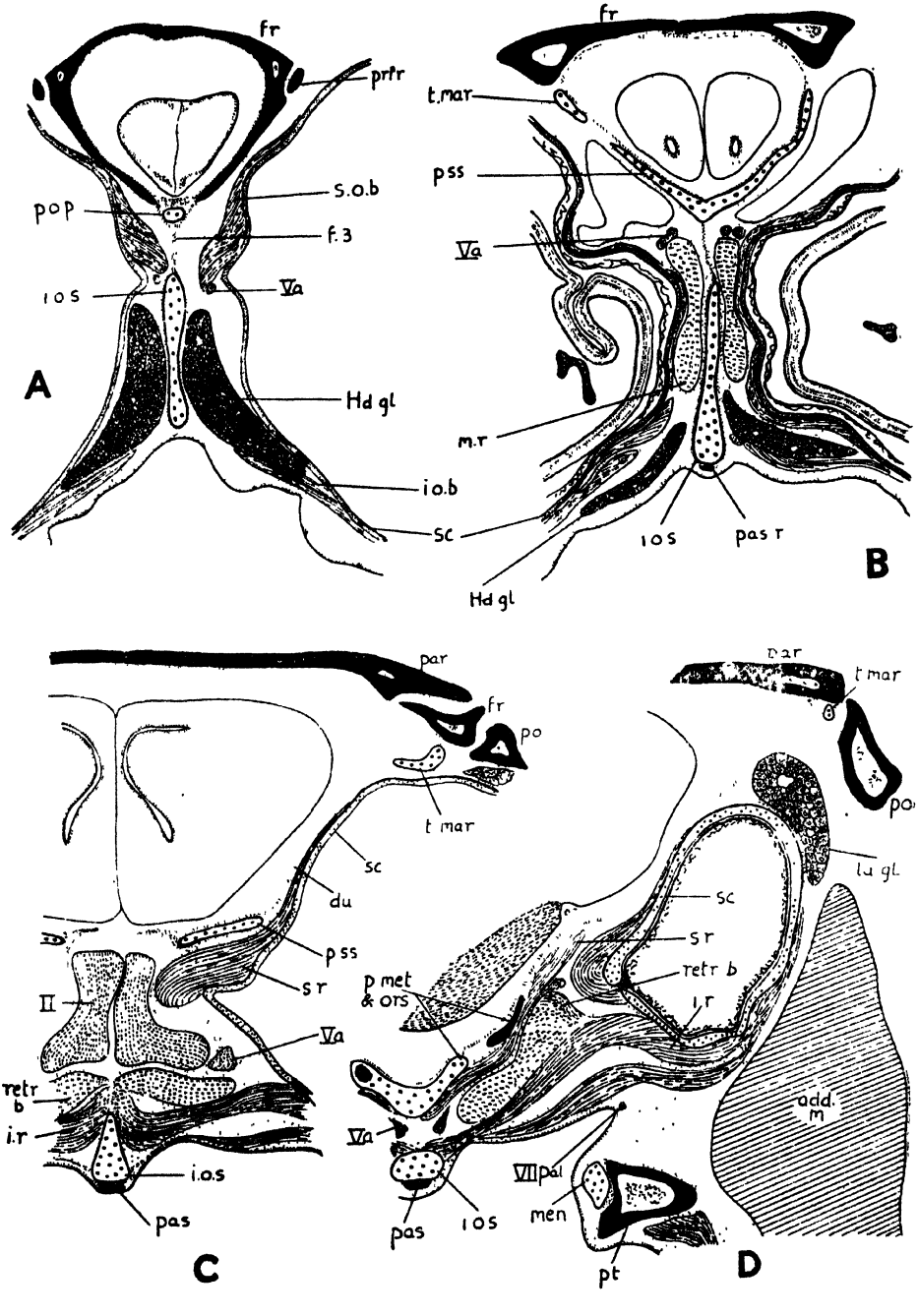
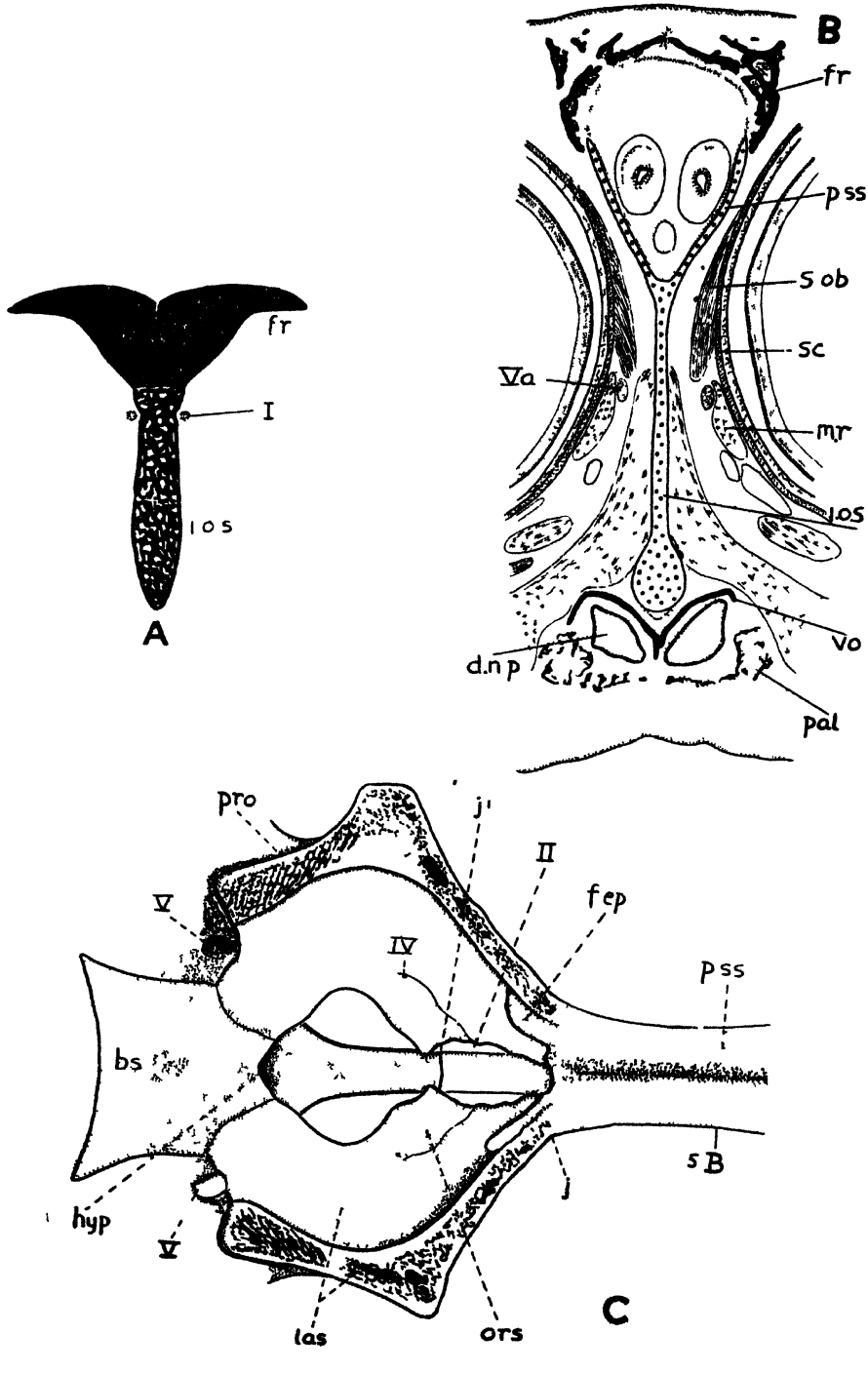


FIG. 4.

A–D. *Varanus monitor*, subadult. Series of transverse sections through head at levels shown in fig. 3. (All × 14.)



For legend see p. 489]

FIG. 5.

The small ossifications which may occur in the anterior brain-case of some reptiles may now be described. When present these only appear fairly late in the life of the individual, and while they are unlikely to be seen in sections of embryos or neonatal specimens, they are also likely to drop out of dried skulls. In adult lizards areas of cartilage in the anterior brain-case become calcified, and in some species are liable to ossify (see Huxley, 1863, whose account of the replacement ossifications in this region in lizards is still the best available in English). In *Iguana* these ossifications are particularly extensive and involve the pila metoptica and adjoining cartilages, together with part of the planum supraseptale and interorbital septum (see fig. 2). Similar conditions have been reported by Camp (1940) in mosasaurs, fossil marine lizards related to the varanids. In living varanids, however, such ossifications appear to be confined to the pila metoptica, even in mature specimens (Bahl, 1937 ; personal observations, fig. 3). Similar ossifications have been described in other lizards by Parker (1880) and Siebenrock (1895, etc.), but it is possible that these workers did not always distinguish between bones and areas of calcified cartilage (see addendum).

In *Sphenodon* and Testudines no parts of the anterior brain-case are known to ossify, but in crocodiles the side walls of the brain-case behind the optic foramina in the region of the pila metoptica and pila antotica become bony (fig. 5C). Similar conditions appear to have been present in dinosaurs (see Osborn, 1912, on *Tyrannosaurus*: Holland, 1903–06, on *Diplodocus*; and many other accounts) and in phytosaurs (Camp, 1930) where the interorbital septum was also partly ossified.

In all living reptiles the trabeculae ossify around the level of the hypophyseal fossa to form the anterior part of the basisphenoid. During the later part of embryonic life perichondral ossification begins in the paired parts of the trabeculae in the region of the hypophyseal fossa. In lizards this ossification is almost from its first appearance intimately related to a thin plate of bone which appears on the ventral aspect of the trabeculae and has usually been regarded as the parasphenoid (see also Kesteven, 1940, etc., cited later). In most reptiles the basisphenoid ossification only just reaches the level where the trabeculae fuse so that the basisphenoid ends in a blunt anterior process. This articulates by single or paired facets either with the cartilaginous trabecula communis or with the persistent unossified portions of the paired trabeculae (figs. 2, 3). Even in adult material the remains of the cartilaginous trabeculae can be seen in microscopic sections extending backwards for some distance into the substance of the basisphenoid. In Crocodilia (and also apparently in dinosaurs and phytosaurs) the basisphenoid ossification extends further forwards into the trabecula communis, where it appears as a vertical blade-like process below and just behind the optic chiasma (fig. 5C). In most forms the parasphenoid rostrum projects forwards beneath the interorbital septum (figs. 2, 3A). In some lizards the rostrum is lacking, while in some turtles this part of the parasphenoid is only present in the embryo and regresses before hatching (Pehrson, 1945).

The nomenclature and homologies of the anterior brain-case ossifications in reptiles deserves comment. The terminology of the side-wall ossifications has already been reviewed by de Beer (1926), and by Shaner (1926), who deals with the nomenclature used in describing fossil forms. Paired ossifications above and immediately behind the optic nerves (i.e. of the pila metoptica, taeniae mediales,

FIG. 5.

A. *Strix* sp. Transverse section of dried skull at mid-orbital level. Approx. position of olfactory nerves is shown The ossified interorbital septum is pneumatised. (×2.)

B. *Alligator mississippiensis*, 26 mm. head-length embryo. Transverse section through brain-case at mid-orbital level, corresponding with position of line 5 B in C below. (×16.)

C. *Alligator mississippiensis*, juvenile. Anterior endocranial brain-case seen from above after removal of frontals and parietals, showing extent of replacement ossifications. The cartilaginous planum supraseptale is shown in thin outline. Based on dried skull and dissection. (×3.6.)

f.ep., unossified region corresponding with position of fenestra epioptica in the chondrocranium. *j.*, junction between laterosphenoid (*las*) and unossified planum supraseptale. *j.*[1], junction between basisphenoid and unossified trabecula communis.

planum supraseptale, etc.) are termed orbitosphenoids; those situated more posteriorly (i.e. ossifications of the pila antotica) have been termed laterosphenoids or pleurosphenoids. These names were introduced to distinguish these ossifications in the true side-wall of the cranial cavity of lower vertebrates from the mammalian alisphenoids which are held by most workers (with the notable exception of Kesteven, 1941, etc.) to represent ossifications in the ascending process of the palatoquadrate, secondarily incorporated into the brain-case (see Gregory and Noble, 1924; Goodrich, 1936).

There is less unanimity regarding the median elements. Any ossification in the interorbital septum of lizards has usually been called a presphenoid (Huxley, 1863; Parker, 1880: Siebenrock, 1895, etc.). Description of such an element as a presphenoid seems undesirable, however, since this term has been more generally used for the trabecular ossification which develops in contact with the basisphenoid in many archosaurs, therapsids and mammals. In Sauria, however, the septal ossification always appears to be separated from the basisphenoid behind by a tract of unossified trabecula communis, and sometimes by portions of the paired trabeculae as well (see fig. 2). The term septosphenoid, introduced by Camp (1940) to describe such ossifications in mosasaurs, is therefore more suitable, while the term presphenoid may be restricted to trabecular ossifications in contact with the basisphenoid behind.

The existence among living reptiles of a presphenoid in the sense defined is doubtful, though such an element has been recognized in dinosaurs (see Shaner, 1926, for discussion) and phytosaurs (Camp, 1940). As previously stated, the portion of the trabecula communis below and immediately behind the optic nerve is ossified in crocodiles, but I have failed to find any suture demarcating it posteriorly from the body of the basisphenoid; in an *Alligator* embryo of 26 mm. head-length the whole of this region was unossified. Camp (1946) has described sutures separating the paired articular facets of the anterior process of the basisphenoid from the rest of the bone in a young specimen of the gecko *Coleonyx*, and regards these as constituting 'a paired presphenoid'. I have, however, been unable to identify separate ossific centres for these facets in sections of *Coleonyx* or other lizards. Kesteven (1940, etc.) has suggested that the element usually regarded as the parasphenoid in lizards and birds is an 'ectochondral' ossification derived from osteoblasts which have migrated from the basisphenoid region, and must therefore be regarded as a presphenoid. In his view the parasphenoid of fishes and amphibia is represented in higher vertebrates by the pterygoid bones. A critical survey of this problem is beyond the scope of the present investigation, but Kesteven's observations make it all the more desirable that Camp's term septosphenoid should replace that of presphenoid for independent ossifications of the interorbital septum.

The complicated and numerous extrinsic eye muscles of Sauropsida arise from the side-walls of the brain-case and interorbital septum, the retractor bulbi group extending their origin back into the hypophyseal region in many forms. There have been few descriptions of the adult topography of these muscles since the observations of Weber (1877) on *Lacerta*. More recently Bruner (1908) has described certain muscles related to the orbital blood sinuses in lizards and turtles, while Säve-Södebergh (1946) has described the retractor bulbi group in *Sphenodon* and several lizards. Pearson (1921) figures the origin of most of the extrinsic eye muscles from the brain-case cartilages in a late embryo of *Lygosoma* (see fig. 2) but her account is hardly complete. Even in forms with a spectacle and no nictitating membrane (e.g. geckos) some components of the retractor bulbi group are apparently present. The absence of these muscles in snakes cannot therefore be correlated with the development of a spectacle.

2. *Sauria, Testudines, etc: development.*

While the morphology of the fully developed chondrocranium of reptiles is now well known, much remains to be learnt about the development in the earlier stages

when the skull is still largely procartilaginous. At present only in the case of *Sphenodon* (Howes and Swinnerton, 1900), *Lacerta* (de Beer, 1930) and certain turtles (Shaner, 1926; Pehrson, 1945) has any systematic investigation of these stages been made. Since a number of sectioned embryos of *Anguis fragilis* and *Lacerta vivipara* were available, certain observations on the development of this part of the skull have been made. These observations suggest that certain processes associated with skull formation deserve greater emphasis than they usually receive in studies of the chondrocranium. The following account refers chiefly to *Anguis*, but conditions in this form were found to differ little from those in *Lacerta*.

The elements of the anterior brain-case chondrify relatively late in development and the framework of the whole region is laid down in procartilage long before any true cartilage has appeared. In this respect the brain-case lags behind certain other parts of the skeleton such as Meckel's cartilage and the bodies of the vertebrae. The median elements of the brain-case (i.e. trabeculae and their derivatives) chondrify rather earlier than the lateral elements (i.e. orbital cartilages, sphenethmoid commissures, etc.)

The first parts of the anterior brain-case to appear are the procartilaginous forerunners of the trabeculae. In *Anguis* embryos of the earliest relevant stages available (c. 3·3 mm. head-length) these are paired throughout much of their extent. In the orbital region, however, they are connected across the midline by a mesenchymatous condensation (Pl. **9**A).

In *Lacerta agilis*, de Beer (1930, 1937) describes the cartilaginous trabeculae as being initially fused in the orbital region at the 3·5 mm. *h*–1 stage. A relatively earlier procartilaginous stage of *L. vivipara* (c. 2·5 mm. *h*–1), however, shows the trabeculae still wide apart in this region (Pl. **10**D). The chondrocrania of both *Anguis* and *Lacerta* may therefore be regarded as initially platytrabic, corresponding with conditions reported in other reptiles (e.g. *Ascalabotes*, Sewertzoff, 1900; *Sphenodon*, Howes and Swinnerton, 1900 and personal observations).

de Beer (1937) has pointed out that the development of the cartilaginous brain-case is closely associated with the formation of the meninges. The mesenchymatous sheath which surrounds the neural tube first differentiates into an ectomeninx and an endomeninx which become separated by areolar tissue. The endomeninx gives rise to the pia-arachnoid, while the ectomeninx subsequently differentiates into an outer perichondral and periosteal layer, and an inner layer which becomes the dura mater. In *Anguis* this differentiation of the ectomeninx seems to occur around the 3·3 mm. *h*–1 stage, where a distinct mesenchymatous condensation has appeared on the lateral aspects of the brain (Pl. **9**A). Subsequently this condensation extends downwards away from the dural layer, and becomes continuous with the condensation surrounding the trabeculae, which at the 3·5 mm. *h*–1 stage have become more closely fused (Pl. **9**B).

In embryos of about 3·8 mm. *h*–1. the fused trabeculae have become more compressed vertically, and are more definitely associated with the ventrally inflected medial borders of the ectomeningeal condensations on either side of the brain (Pl. **9**C). At this stage the trabecula communis is becoming procartilaginous. Rather later (c. 4·2 mm. *h*–1 : Pl. **9**D) the sphenethmoid commissures and orbital cartilages begin to chondrify in these lateral condensations. The two elements are directly continuous and their medial edges are inclined steeply downwards to join the trabecula communis. In this way the definitive interorbital septum is developed entirely from the fusion of the posterior parts of the sphenethmoid commissures and orbital cartilages above, with the trabeculae below. No evidence for the appearance of an independent median plate, as was suggested by de Beer for *Lacerta agilis*, was found.

At the 4·2 mm. *h*–1 stage the interorbital septum in *Anguis* is unfenestrated, and its upper part, derived from the lateral elements, still shows traces of paired origin where the downturned edges of the orbital cartilages have failed to fuse completely with each other (Pl. **9**D).

At the 4·5 mm. *h*–1 stage (Pl. 10A) the interorbital septum and lateral elements are almost entirely cartilaginous; as far as can be seen, the latter chondrify in continuity with the former. The sphenethmoid commissures are now continuous anteriorly with the roof of the nasal capsule, while posteriorly they run back for some distance in continuity with the interorbital septum, and merge into the orbital cartilages which widen out on either side to form the planum supraseptale.

In subsequent stages of *Anguis* (5·2 mm. *h*–1 : fig. 6A, Pl. 10B) the orbital cartilages become more extensive laterally and come to lie in a more horizontal plane, forming the wings of the planum supraseptale, which are never very extensive in this species. Continuity between the orbital cartilages and the trabeculae is interrupted at the level of the optic nerve foramina, where the interorbital septum ends and the paired trabeculae pass backwards on either side of the hypophysis to join the basal plate.

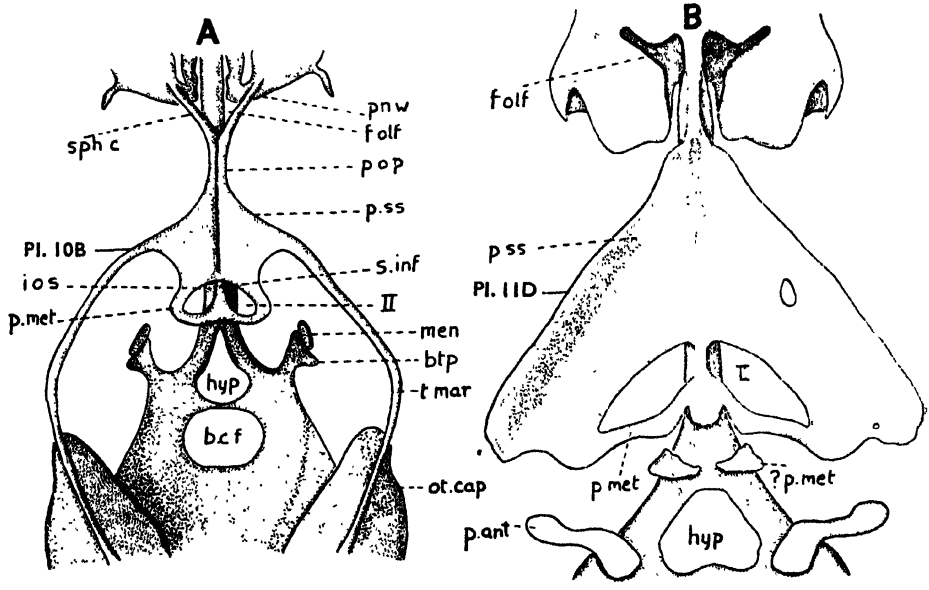


FIG. 6.

A. *Anguis fragilis*, 5·2 mm. head-length embryo. Graphic reconstruction of anterior endocranial brain-case in dorsal view. This reconstruction differs in some respects (e.g. position of basitrabecular processes) from that figured by Zimmerman (1914) of a slightly later embryo.

B. *Chelydra serpentina*, 10 mm. head-length embryo. Graphic reconstruction of anterior endocranial brain-case in dorsal view. The pila antotica are separate from the rest of the orbital cartilages at this stage. In this and other respects the reconstruction shown differs from that figured by Nick (1912) of a " ripe " embryo of *Chelydra*.

?p.met., nodule of cartilage possibly connected with pila metoptica at an earlier stage. (A × 22 : B × 18.)

In these later stages (4·5–5·2 mm. head-length ; Pl. 10A, B) the ectomeninx has come to form a rather sharply defined dural membrane around the brain, and the mesenchymatous condensation on its outer surface has largely disappeared. The perichondrium surrounding the lateral cartilage elements is continuous internally with the dura. In the dorsal region the frontals and parietals ossify in membrane on the external aspect of the dura, and spread downwards on either side of the brain to make contact with the lateral margins of the orbital cartilages. Behind the level of the optic foramina, however, the greater part of the side-walls of the brain-case are formed only by dural membrane, reinforced by the taeniae marginales and pila metoptica, the only orbito-temporal bars present in *Anguis* (fig. 6A).

The development of fenestrae in the interorbital septum raises certain problems of interest, and begins around the 4·5 mm. *h*–1 stage (Pl. **10** A). In *Anguis* fen. 1 is incomplete dorsally and the septum in this region is lower and thicker than in *Lacerta*. In the latter species both fen. 1 and fen. 2 appear to arise by resorption of cartilage in the trabecular part of the septum, fen. 1 appearing earlier than fen. 2. In *Anguis*, fen 2 arises in the same manner as in *Lacerta*, while in both species fen. 3 originates by absorption of the downturned medial parts of the orbital cartilages (Pl. **10** A, B). In all cases the two layers of the perichondrium which surround the disappearing cartilage fuse to form a membranous sheet which fills up the fenestrae.

The factors responsible for the appearance of these fenestrae have been discussed by Rice (1920) in his account of the chondrocranium of *Eumeces*. He follows the lead of Gaupp (1900) in emphasizing the pressure exerted by the developing eyes. The fenestrae are, however, present and relatively large in some small-eyed lizards such as *Anniella* (fig. 1 B) and *Nessia*; they were also found in the normal situations in an anomalous micropthalmic embryo of *Lacerta vivipara*, where the interorbital septum, though lower than in a normal sibling, was well developed. Moreover an unfenestrated septum is present in some turtles and in crocodiles where the eyes are relatively as large as in many lizards.

It was thought possible that the appearance of the fenestrae might be related to the development of the extrinsic eye muscles. In adult lizards the superior and inferior oblique muscles were found to arise constantly from the membrane filling in fen. 1 (when present) and fen. 2 (see fig. 2). No muscles were, however, observed to arise from the membrane of fen. 3, which is by far the most extensive of the three fenestrae. The significance of this fenestration remains obscure, and it is probably best regarded as being an expression of the same factors which have been responsible for the reduction of the floor and sides of the brain-case in lizards.

Data on the embryonic stages of *Sphenodon* and Crocodilia suggest that in these forms the development of the brain-case follows the same pattern as in lizards. The earliest relevant stage of *Sphenodon* in the Dendy collection (fig. 7 C) shows the still paired trabeculae connected across the midline by a mesenchymatous condensation, much as in *Anguis*. Later stages indicate that, as in lizards, the septum is derived from the fusion of the orbital cartilages above with the trabecula communis below, and later undergoes secondary fenestration (fig. 7 D-F). A single relatively early stage (7·5 mm. *h*–1) of *Crocodilus* (fig. 7 A) shows a low broad interorbital septum, the lower part of which shows evidences of paired trabecular origin. Subsequently the septum becomes high and narrow, as in the late *Alligator* embryo shown in fig. 5 B.

Conditions in Testudines appear to differ from those in other reptiles in that a third cartilaginous element, the intertrabecula, contributes to the interorbital septum. The intertrabecula, first observed by Parker (1880) in *Chelone*, has recently been studied in other forms by Pehrson (1945). The origin and significance of this structure, and its relationship with the taenia intertrabecularis which divides the hypophyseal fossa longitudinally in some forms (see de Beer, 1937) are still imperfectly understood.

Pehrson states that the trabeculae are initially separate in the orbital region in *Dermochelys* and *Lepidochelys*, and similar conditions have been described by Shaner (1926) in *Chrysemys*. Subsequent stages of *Lepidochelys* show that the trabeculae do not fuse to form a trabecula communis, as in lizards, but remain separated by the intertrabecula, a longitudinal bar of cartilage which develops from the mesenchymatous tissue between the trabeculae. At the 15 day stage of *Lepidochelys* figured by Pehrson the intertrabecula appears as a wedge-shaped structure lying between the trabeculae, and is apparently connected above with the downturned medial borders of the ectomeningeal condensations which later become the orbital cartilages. The later growth processes are difficult to follow from Pehrson's account, and he does not discuss the contributions made by the orbital cartilages to the interorbital septum. From his data and figures it appears, however, that the intertrabecular tissue grows up dorsally between the trabeculae and fuses with the orbital cartilages to form the

greater part of the interorbital septum. The trabeculae, separated by the intertrabecula, become thinner, and at the 19 day stage form two vertical plates which are closely applied to the sides of the lower part of the interorbital septum. Corresponding conditions were observed by Pehrson in *Chrysemys*, but in *Dermochelys* the anterior parts of the trabeculae approach one another more closely and the intertrabecula can hardly be recognized as a distinct structure.

My own stages of *Chelydra serpentina* are not sufficiently numerous and closely spaced to allow the development of the interorbital septum to be followed completely, but they appear to confirm the essential features of Pehrson's account. At the 5·5 mm. head-length stage Pl. **11** A) the intertrabecula appears as a wedge-shaped formation sandwiched between the trabeculae, the outer borders of which stain deeper than the rest. Dorsally, both the trabeculae and the intertrabecula appear to be continuous with the lower ends of the orbital cartilages. At the 6 mm. *h*–l stage (Pl. **11** B) the formation of the interorbital septum is considerably more advanced, and the skeleton of this region has become cartilaginous and resembles the 19 day stage of *Lepidochelys* figured by Pehrson. The ventral part of the septum still shows the ridged appearance described by Pehrson ; the lateral ridges with their darkly staining borders (also shown in Pehrson's figure) presumably represent the remains of the trabeculae, while the median ridge is formed by the intertrabecula. Both trabeculae and intertrabecula are continuous above with the orbital cartilages, so that it is impossible to define their limits at all precisely. The appearance suggests, however, that cartilage derived from the intertrabecula has grown up between the orbital cartilages to form the central part of the septum. This appearance is perhaps more marked in two later stages (9 and 10 mm. *h*–l respectively) where the trabeculae can no longer be distinguished at all and the interorbital septum is approaching the condition of maturity fig. 6 B, Pl. **11** C, D). The different regions of the septum in these figures have been labelled to correspond with this interpretation, which must be regarded as provisional.

The significance of the intertrabecula and its possible occurrence in other reptiles is discussed by Pehrson. He suggests that the formation of this structure may occur during ontogeny in any form where the trabeculae do not fuse to give rise to a trabecula communis. In turtles the intertrabecula appears to arise from tissue corresponding in position with the mesenchymatous condensation between the trabeculae of other reptiles at the stage when these are still paired (e.g. *Anguis*, Pl. **9** A ; *Sphenodon*, fig. 7 C). It is possible that the subsequent development of this structure is inhibited by the early fusion of the trabeculae, as Pehrson implies may be the case in *Dermochelys*. The intertrabecula has not, however, been observed in snakes where the chondrocranium remains platytrabic throughout life and where the mesenchymatous condensation between the trabeculae is particularly well marked. The small nodule of cartilage between the trabeculae of a *Python* embryo might, however, be interpreted along the lines suggested by Pehrson (see later).

The previous observations on the development of the interorbital septum in reptiles, incomplete though they are, allow certain generalizations to be made. In all the forms considered the chondrocranium is initially platytrabic, and (with the modifications described in turtles), becomes tropitrabic later in development. The orbital cartilages arise in ectomeningeal condensations, the medial edges of which are bent downwards to join the trabeculae. In most forms the interorbital septum is derived from only two distinct cartilaginous elements, the orbital cartilages above, and the trabeculae below. In most turtles, however, a third element, the intertrabecula, appears between the trabeculae and also fuses with the orbital cartilages, probably giving rise to the central part of the interorbital septum. The origin and significance of the intertrabecula are obscure. In some forms the interorbital septum becomes fenestrated during the course of development : this fenestration is the result of secondary absorption of cartilage, and probably occurs at the site of fusion between the orbital cartilages and trabeculae.

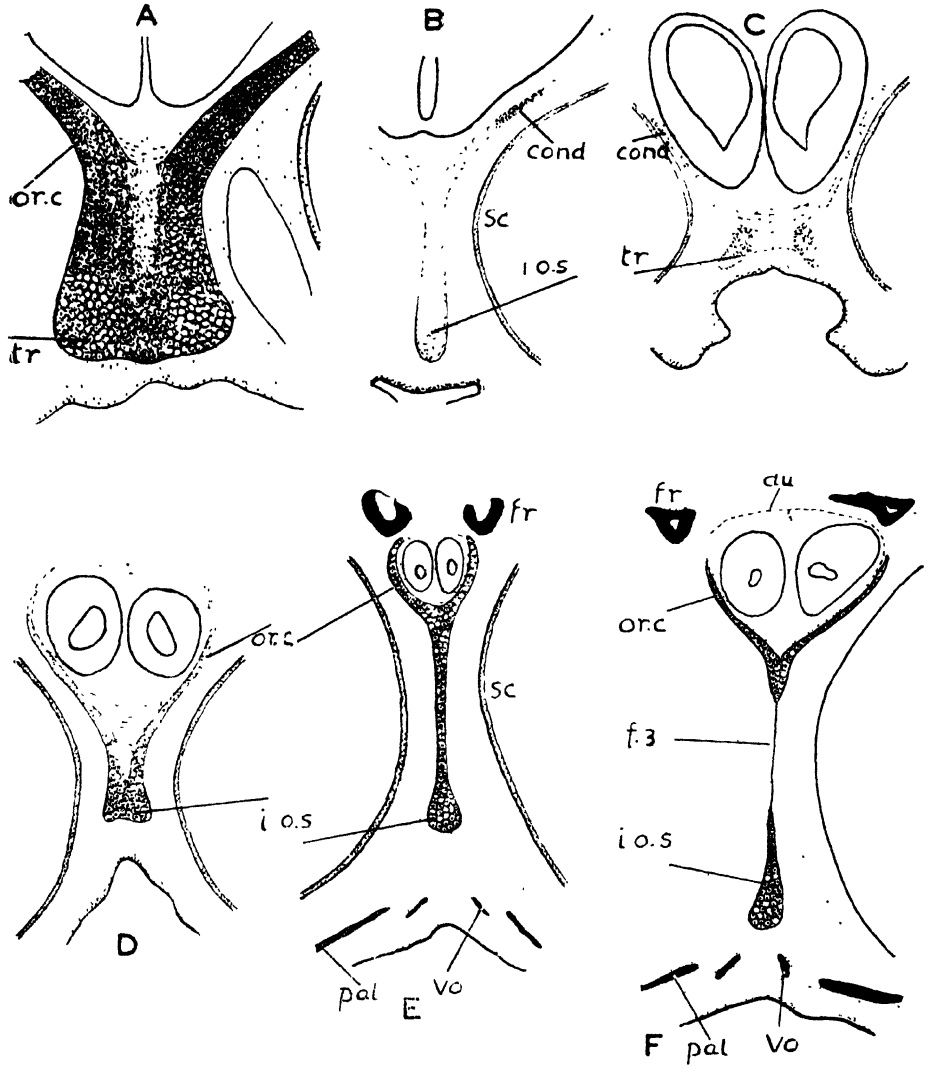


FIG. 7.—Transverse sections through mid-orbital region showing development of interorbital septum in crocodiles, birds and rhynchocephalians.

A. *Crocodilus niloticus*, embryo, 7·5 mm. head-length. Orbital cartilages have fused with trabeculae, but not completely with each other, so that upper part of septum is still paired (cf. fig. 5B of a 26 mm. *h*–1 *Alligator embryo*.

B. *Passer* sp., embryo. Procartilaginous interorbital septum continuous above with ectomeningeal condensation, one part of which appears to be procartilaginous.

C. *Sphenodon punctatum*, embryo, Dendy stage P.39*a*. Procartilaginous trabeculae still paired, and continuous above with ectomeningeal condensation.

D. *Sphenodon*, embryo, Dendy stage PQ.50*a*. Trabeculae and orbital cartilages fusing to form septum.

E. *Sphenodon*, embryo, Dendy stage R.144. Interorbital septum high and narrow. Orbital cartilages completely fused.

F. *Sphenodon*, embryo, Dendy stage R.141. Appearance of fenestra 3 by secondary resorption of septal cartilage, as in *Anguis* (Pl. 10A, B).

cond., ectomeningeal condensation foreshadowing appearance of orbital cartilage (*or.c.*).

3. *Aves.*

The avian brain-case appears to be a specialized derivative of the archosaurian pattern. The chondrocranium is highly tropitrabic and a well developed interorbital septum is present, which is ossified in most forms, though it may undergo pneumatisation (as in *Strix*, fig. 5A). The complex ossifications which develop in the septum probably include both septosphenoid and presphenoid elements. Since these

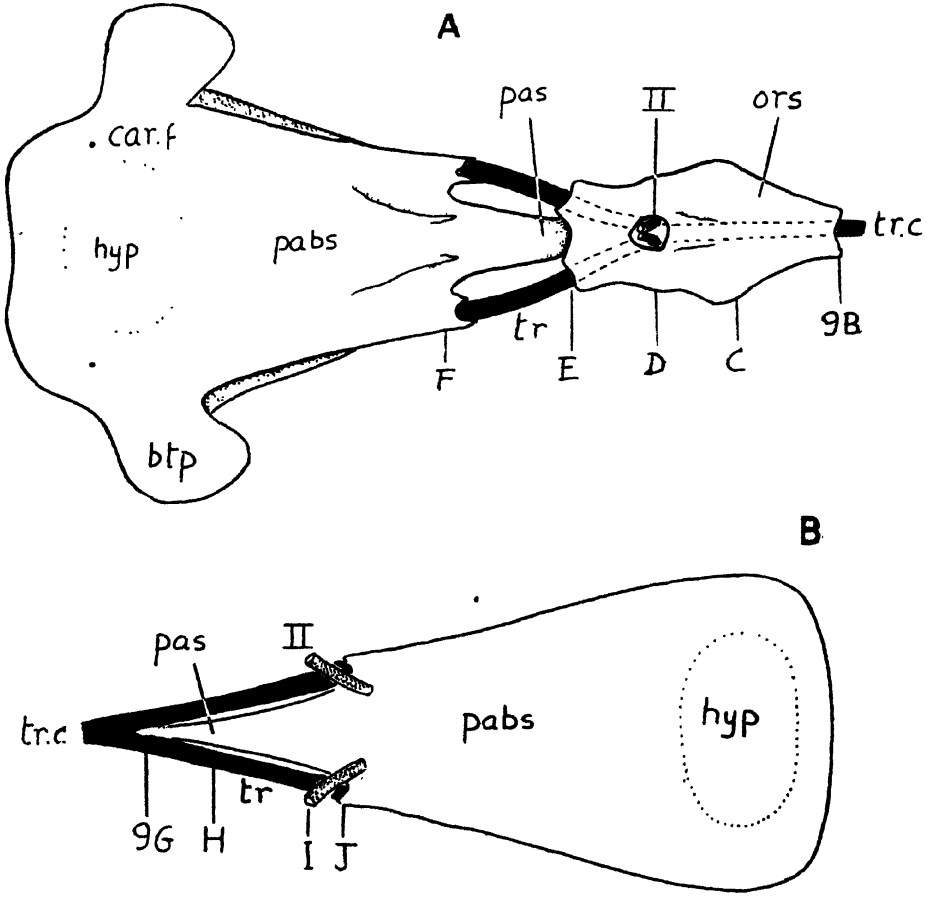


FIG. 8.

A. The amphisbaenid *Trogonophis wiegmanni*, adult. Reconstruction of floor of brain-case seen from above. The optic nerves pass through foramina in the orbitosphenoids (*ors.*) See also fig. 9D. (×28.)

B. The burrowing snake *Rhinophis philippinus*, adult. Reconstruction of floor of brain-case seen from above. The optic nerves pass dorsal to the parabasisphenoid (*pabs*), through foramina in the frontals. See also fig. 9I, J. (×32.)

Trabeculae shown in black. Levels of section in Fig. 9 shown.

ossifications only exist as separate bones for a short time during the life of the individual, appearing late in ontogeny and losing their sutural boundaries before adult life, their interpretation is difficult and does not appear to be well understood (see de Beer, 1937, for review of literature).

The work of de Beer and Barrington (1934) on *Anas* shows that at one stage of ontogeny the orbital cartilages are extensive, resembling the condition in crocodiles. Subsequently, however, these cartilages undergo marked regression and no longer support the olfactory nerves, which in the adults of most birds pass through the orbits, grooving the septum on either side (e.g. in *Strix*, fig. 5A). Such changes are probably associated with the development of very large eyes and reduction of the olfactory system. Only in *Apteryx* among living birds is the interorbital septum absent; in this nocturnal form the eyes are small, and the nasal capsule which extends back between them is correspondingly larger (T. J. Parker, 1891; de Beer, 1937).

As in reptiles the chondrocranium is initially platytrabic, but a single embryonic stage of *Passer* (fig. 7B) shows the trabeculae fused to form a high interorbital septum which is still procartilaginous. The orbital cartilages in this specimen are represented only by mesenchymatous condensations similar to those in the 3·3 mm. *h*–1 embryos of *Anguis*. No adequate study of the development and ossification of the interorbital septum in birds appears to have been made.

4. *Amphisbaenidae.*

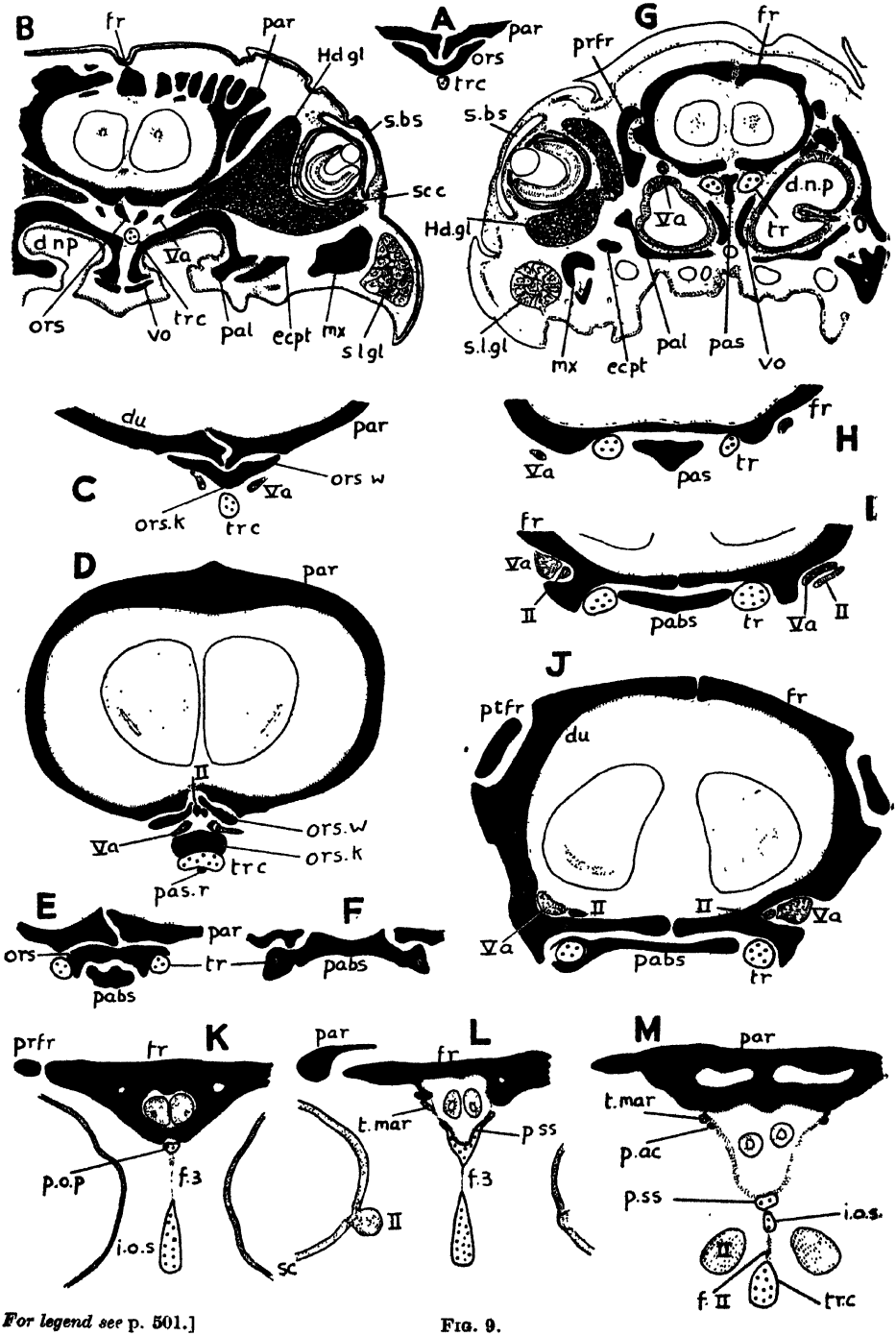
This group of highly specialized burrowing reptiles has generally been referred to the suborder Sauria (e.g. Camp, 1923; Romer, 1945). Zangerl (1944), however, has suggested as a result of his osteological studies that this group is not closely related either to lizards or snakes, but should be placed in an order of its own.

Embryological stages of amphisbaenids have never been examined, and the nature of the different elements of the brain-case must be deduced from adult anatomy. Serial sections through the heads of two specimens of *Trogonophis wiegmanni* (figs. 8A, 9B-F), and through the orbital region only of an example of *Amphisbaena fuliginosa* (fig. 9A) were available. They form the basis of the following account.

In the nasal region the trabeculae are fused to form a nasal septum, as in Squamata, but further back no interorbital septum in the true sense is present, as was noted by Fischer (1900). As in burrowing snakes such as *Typhlops* (fig. 1D) and *Rhinophis* (fig. 9G, etc.) the whole width of the brain and parts of the nasal cavities intervene between the two orbits. The trabeculae, which remain cartilaginous in the adult, are fused in the orbital region to form a single trabecula communis situated between the upper borders of the funnel shaped palatines (fig. 9B). Immediately above the trabecula communis in the floor of the cranial cavity at the posterior orbital level is a bone consisting of two slightly upturned lateral wings meeting in the midline to form a broad ventral keel (figs. 8A, 9A, C; a similar condition is shown in *Monopeltis* by Kritzinger, 1945). Further back the optic nerves pass between the wings and the keel to enter the cranial cavity as has been previously described. Behind this level first the wings and then the keel terminate abruptly (fig. 8A). At the level of the optic foramina, a slender rod, regarded as the parasphenoid rostrum, appears in the midline beneath the trabecula communis and is continuous posteriorly with an extensive ossification which surrounds and invades the trabeculae as in other reptiles (fig. 9F).

There can be little doubt that Zangerl's interpretation of this region is essentially correct, and that the two lateral wings of the bone first described represent the fused orbitosphenoids, ossified in the two halves of the planum supraseptale. The relationship of the optic nerves to these elements (which was not described by Zangerl) would in itself, seem to render this interpretation certain.

The identity of the keel between the two orbitosphenoid wings is, however, less obvious. Zangerl states that in amphisbaenids generally the parasphenoid does not carry a rostrum, and that in its place is a slender element in front of the basisphenoid which he regards as a presphenoid. Study of his figure of *A. fuliginosa* suggests that his presphenoid corresponds in position with the keel described. The relationship of this structure to the optic nerves in *Trogonophis* suggests that it represents an ossification of the dorsal part of the trabecula communis (or posterior extension of the interorbital septum) which lies immediately below the optic chiasma in lizards



For legend see p. 501.]

FIG. 9.

(figs. 2, 9M), the ventral part of the trabecula communis remaining unossified. In this case it can be regarded as a presphenoid, as Zangerl suggests. The difficulty of accepting this interpretation lies in the relationship of this keel to the unossified parts of the paired trabeculae (fig. 9E). The presphenoid is, by definition, a trabecular ossification but at this level the trabeculae remain cartilaginous into adult life and lie on either side of the keel, so that it is difficult to see how they could have contributed to the latter ossification. Nor does it seem likely that the keel could have arisen as an anterior extension of the basisphenoid (as Kesteven, 1941, suggests is the mode of development of the bone usually regarded as the parasphenoid rostrum in Sauropsida) since it is not continuous with the basisphenoid posteriorly. Another possibility is that the whole element in question corresponds with the orbital cartilages of lizards, the wings representing the ossified planum supraseptale, and the keel the downturned medial edges of the orbital cartilages which in lizards contribute to the interorbital septum.* It may be noted that if this homology is correct the optic nerves pass through foramina in the orbitosphenoids, and not between orbitosphenoids and presphenoid (as in mammals), or between orbital cartilages and trabecula communis (as in lizards). The possibility of an intertrabecular ossification (see conditions in turtles) must also be borne in mind. It is clear that no complete interpretation of the amphisbaenid brain-case can be made until suitable embryonic stages are available. Why the trabeculae, alone among the brain-case elements, should fail to ossify in these strange reptiles, is, of course, a matter for question (see addendum).

There seemed no difficulty in recognizing a parasphenoid rostrum in *Trogonophis*, in spite of Zangerl's statement to the contrary. This is present in the usual reptilian position beneath the trabecula communis (fig. 9D), and becomes continuous with the basisphenoid behind, forming a parabasisphenoid. The latter widens out posteriorly and becomes flattened (fig. 9F), and, as in lizards it carried basitrabecular processes which articulate with the pterygoids by meniscus cartilages. Laterosphenoids are also present above the trigeminal ganglia, as described by Zangerl.

The Amphisbaenidae possess a well ossified endocranial brain-case, which, though limited to the ventral aspect of the cranial cavity, is, as Zangerl points out, quite as well developed as in salamanders, extending both in front of, and behind, the optic foramina. In this respect the group is peculiar among living reptiles, and can, in particular, be sharply distinguished from both Sauria and Serpentes.

It may be objected that this feature constitutes a burrowing adaptation of little phylogenetic significance. Comparison with burrowing lizards such as *Anniella* and burrowing snakes such as *Rhinophis*, however, does not support this objection. In those forms, as in amphisbaenids, strength of the skull has been provided by the massive structure of the dermal bones and by the presence of interlocking sutures in the cranial roof. In neither the lizards nor the snakes, however, is there any

* This interpretation has been followed in the lettering to fig. 9A–F.

FIG. 9.

A. *Amphisbaena fuliginosa*, adult. Transverse section through fused orbitosphenoids at mid-orbital level. (×12.)

B. *Trogonophis wiegmanni*, adult. Transverse section through head at mid-orbital level (see fig. 8A). (×21.)

C–F. *Trogonophis*. Series of transverse sections showing floor of brain-case at higher magnification than B. Levels are shown in fig. 8A. (×30.)

G. *Rhinophis philippinus*, adult. Transverse section through head at mid-orbital level (see fig. 8B). (×32.)

H–J. *Rhinophis*. Series of transverse sections showing floor of brain-case at higher magnification than G. Levels are shown in fig. 8B. (×50.)

K–M. The pygopodid lizard *Lialis burtoni*, adult. Transverse sections through anterior brain-case showing relationship of endocranium to frontals and parietals. (×11.)

ors.k, *ors.w*, orbitosphenoid keel and wings.

tendency to ossify the interorbital chondrocranium. The presence of such ossification in the Amphisbaenidae would seem to justify Zangerl's view that this group should receive a more distinct taxonomic status.*

5. Serpentes.

The orbital brain-case of snakes differs widely from that of the reptiles previously described. The nasal region is on the whole similar to that of lizards with a high nasal septum formed from the fused trabeculae. The latter do not fuse in the orbital region, however, and the chondrocranium remains platytrabic throughout life. The resulting prominence and disposition of the trabeculae is most characteristic (see figs. 1E, 9G–J, Pl. **10**C, E), and it is perhaps hardly surprising that these structures were first discovered in a snake (Rathke, 1839).

As compared with most lizards there appears to have been some relative shortening of the anterior part of the skull in snakes, and this, combined with the presence of a ductus nasopharyngeus is responsible for the extension of the nasal sacs back to the mid-orbital level (fig. 1E, F). This condition is approached, however, by certain lizards and by amphisbaenids. In the Typhlopidae (fig. 1E: Haas, 1930) this telescoping of the front of the head has been associated with extreme reduction of the eyes, so that a section through the middle of the orbits passes through the trabecula communis and not through the paired trabeculae, as in other snakes.

Apart from the trabeculae, no other elements of the endocranial brain-case are present in the orbital region of adult snakes. In embryos, however, the mesenchymatous condensation around the ectomeninx is well developed, and from this a band of cells stretches down in the midline to blend with the condensation around the trabeculae as is shown in Pl. **10**C of an 8 mm. head-length *Natrix* embryo. This condensation was apparently described as a membranous interorbital septum by Gaupp (1906) in a *Natrix* embryo of similar age.

Parker (1879) described and figured a pair of small unfused orbitosphenoids situated apparently in the lower parts of the ectomeningeal condensation of a *Natrix* embryo, and remarked that these were 'In that arrested chondrocranium mere patches of what is seen in *Lacerta*'. Peyer (1912), Brock (1930) and Bäckström (1931) all reported their inability to find traces of endocranial elements in this region in embryos of *Vipera aspis*, *Leptodeira hotamboia* and *Tropidonotus* (*Natrix*) *natrix* respectively. Recently, however, Parker's findings have been partly confirmed by Bellairs (1949a) who figured and briefly described a pair of cartilaginous nodules above the trabeculae at mid-orbital level in a 7·2 mm. embryo of *Vipera berus*. These structures were not present in the earlier and later embryonic stages of this species available, and it seems likely that they are only present for a short period in the life of the embryo. Another example of an endocranial rudiment in this region is shown in Pl. **10**E of a section of a 12 mm. head-length embryo of *Python molurus*. Here a small nodule of cartilage can clearly be seen in the midline above the paired trabeculae, and is situated in the region corresponding with the position of the 'membranous interorbital septum' observed by Gaupp in his *Natrix* embryo.

While it appears very probable that these cartilaginous nodules represent rudiments of the saurian orbital cartilages, the possibility that the structure shown in the python embryo might correspond with the intertrabecula described by Pehrson in turtles cannot be entirely excluded. In the python, however, this nodule is quite distinct from the trabeculae and appears to be undergoing regression, whereas the chelonian intertrabecula is intimately fused with these structures during the early stages of chondrification. Moreover, the nodule in the python embryo is situated between

* The danger of assessing phylogenetic relationships on the basis of isolated morphological features is well known, and Zangerl's original view (1944) denying the Amphisbaenidae any close relationship with lizards and snakes seems too extreme. In a later paper on the post-cranial skeleton (1945), Zangerl suggests that the group should be placed '*incertae sedes*' with the Squamata. The numerous resemblances between the vomeronasal apparatus and palatal morphology of amphisbaenids and lizards suggest that the former, if not lizards, are at any rate allied to them.

the dorsal parts of the trabeculae only, and does not extend downwards between them as does the intertrabecula in *Lepidochelys* and *Chelydra* (Pl. 11 A, B). It seems more likely, therefore, that the first explanation is correct, and that this spicule of cartilage in the python embryo corresponds with the fused parts of the orbital cartilages in the lizard (i.e. the upper part of the interorbital septum); the paired nodules in the viper may be regarded as unfused rudiments of the orbital cartilages, as was originally suggested. On this interpretation, the endocranial side-walls of lizards would have some parallel in the embryos of snakes.

Later embryonic stages of *Python* were not available, but rudiments of orbital cartilages were searched for unsuccessfully in serial sections of a number of embryos of different species, including several stages of *Natrix natrix*, and of adults or subadults of a number of forms generally regarded as primitive (see terminal list).

The morphology of the posterior part of the orbitotemporal side wall in snakes is not entirely understood (see de Beer, 1937) and was not studied in this investigation, although it is hoped to attempt this problem later. The existence of laterosphenoids is very doubtful. As Peyer (1912) has pointed out, the endocranial brain-case throughout the orbito-temporal region has been entirely replaced by downgrowths from the frontals and parietals, which completely surround the brain in all snakes (see figs. 1 D, E, 9 F, etc.). It is of some interest that the parietal downgrowths ossify later during ontogeny than the frontal downgrowths. The phylogenetic significance of these features of the ophidian skull will be discussed later.

The parasphenoid rostrum is present in snakes; the wings and body are absent, or, at any rate, cannot be distinguished from the basisphenoid. The identity of the rostrum seems certain; in *Natrix natrix* and *Vipera berus* it ossifies from an independent centre beneath the trabeculae, and sends up a lamella of bone between them (Bäckström, 1931: personal observations). This ossification later grows backwards to fuse with the basisphenoid, forming a parabasisphenoid. The trabeculae lie on either side of the rostrum, and are exposed on the ventral surface of the skull for part of their length. The posterior ends of the trabeculae ossify to contribute to the basisphenoid, and their persistent cartilages are received in bony canals as in lizards and amphisbaenids. In some snakes, especially some rather primitive forms such as *Rhinophis philippinus* (figs. 8 B, 9 G–J) and *Eryx conicus*, the vertical lamella which passes up from the parasphenoid rostrum between the trabeculae is large and projects forwards dorsally for a short distance above the trabecula communis. Further back between the paired trabeculae the upper edge of the rostrum bears two short wings which are closely related to the fronto-parietal downgrowths (fig. 9 H). The appearance of the bone in this region, consisting as it does of two lateral wings and a keel, is rather similar to that of the fused orbitosphenoids of amphisbaenids (compare fig. 9 H of *Rhinophis* with 9 C of *Trogonophis* and 9 A of *Amphisbaena fuliginosa*). This similarity suggested that the element usually regarded as the parasphenoid in snakes might in fact represent (or at least include) the fused orbitosphenoids. Study of the relationship of the optic nerves to this element, however, clearly demonstrates that the bone in snakes is correctly identified as the parasphenoid. In *Rhinophis* (figs. 8 B, 9 I, J) the optic nerves pass dorsal to the element in question through foramina in the frontals. In amphisbaenids, on the other hand, the optic nerves pass between the wings and the keel of the element regarded as the fused orbitosphenoids, as has previously been described. In *Rhinophis* and other snakes the ophthalmic nerves pass with the opic nerves through foramina in the frontals, or between the frontals and parietals, and then pursue an extra-dural course back to the trigeminal ganglion. In amphisbaenids and lizards, however, the ophthalmic nerves remain external to the brain-case, passing backwards on either side of the keel or the septum to reach the ganglion. In lizards this structure lies in the cavum epiptericum; in amphisbaenids the epipterygoid is not present but the trigeminal ganglion lies outside the cranial cavity, on the external aspect of the laterosphenoid, which constitutes the endocranial side-wall in this region. In snakes the loss of the endocranial wall and the development of fronto-parietal downgrowths has resulted in the disappearance of the cavum

epiptericum, which is presumably represented by the space between the dura and the parietal downgrowths.

The extrinsic eye muscles of snakes have not been adequately described. These muscles arise from the connective tissue sheath which surrounds the trabeculae and parasphenoid rostrum and in some cases pass through the substance of the Harderian gland (fig. 1E). No instance of their attachment having been transferred to the fronto-parietal downgrowths could be found. The retractor bulbi group of muscles is apparently absent.

Discussion.

From the previous account it will be seen that in the most primitive tetrapods the endocranial brain-case was ossified as far forwards as the nasal capsule, and formed a complete investment for the brain and olfactory nerves. The chondrocranium was apparently tropitrabic, the orbits being separated by a septum which in the adult formed part of the sphenethmoid ossification. Subsequent modifications of this primitive pattern have fallen into two distinct trends: (1) a progressive reduction of the endocranial skeleton of the anterior brain-case, followed in some cases by a compensating development of the membrane bones of the cranial roof, and (2) a sinking down of the brain-case between the orbits with reduction and loss of the interorbital septum, generally associated with failure of the trabeculae to fuse behind the nasal region.

Both these trends have occurred, apparently by parallel evolution, among several groups of amphibia, including the ancestors of all the living orders. The second of these trends does not appear to have been evident in those forms near the line of evolution leading to reptiles. At an early stage in reptilian history, however, the replacement ossifications of the anterior brain-case became reduced. This tendency has been most marked among the lizards and snakes where the chondrocranium also has undergone reduction; it is least apparent in the archosaurs and their avian descendants, and in the Amphisbaenidae. In the case of the amphisbaenids and the birds we are faced with the alternatives of supposing either that they were derived from forms in which the endocranial ossifications had not undergone extensive reduction, or that these ossifications have actually been re-developed.

The changes in the pattern of the chondrocranium may now be discussed; they appear to have considerable bearing on certain problems of squamate evolution. The most primitive reptiles apparently inherited the tropitrabic condition from their labyrinthodont ancestors, and a tropitrabic chondrocranium is characteristic of most modern reptiles, where it is usually associated with the presence of an interorbital septum. The latter structure is derived during ontogeny from the fusion of the orbital cartilages above with each other and with the trabeculae below. In turtles an additional cartilaginous element, the intertrabecula, contributes to the interorbital septum in the embryo, but the adult condition resembles that of other tropitrabic forms.

Two groups of modern reptiles, the Amphisbaenidae and the Serpentes, have departed from the primitive condition. In the Amphisbaenidae the chondrocranium has remained tropitrabic, for the trabeculae, and apparently the orbital cartilages also, are fused in the midline in the orbital region (fig. 9B, etc.). The great reduction in eye size, however, is associated with a change in the relative position of the cranial cavity, which has sunk down between the orbits so that these are no longer separated by a septum. In the snakes the level at which the trabeculae fuse to form a trabecula communis has apparently shifted forwards so that the trabeculae are paired throughout the greater part of the orbital region (figs 1E, 9H–J, etc). The condition in the specialized burrowing snake *Typhlops* (fig. 1D) where the trabecula communis appears at the mid-orbital level has already been described.

Gaupp (1900) regarded the presence of the interorbital septum as being related to the sizes and positions of the principal structures in the vicinity: the nasal capsule, forebrain, and above all, the eyes. In Sauropsida where the interorbital septum is

most extensive, as in the birds and chamaeleons, the eyes are very large, and the nasal capsule and olfactory lobes do not encroach on the interorbital region. In lizards where the septum is low such as *Nessia* and *Anniella*, and in amphisbaenids where the interorbital septum in the sense defined does not exist, the eyes are reduced and the forebrain and parts of the nasal capsule lie between the orbits. In snakes the orbits are relatively large in many forms, and are only partly separated by the cranial cavity and ductus nasopharyngeus (fig. 1 E). The interorbital septum, however, is entirely absent, and except in *Typhlops* (fig. 1 D) and perhaps in allied forms, the trabeculae are paired in the mid-orbital region. As Brock (1941) has observed, this feature appears to constitute a sharp distinction between snakes and all lizards where the chondrocranium is known.

The conditions just described must be considered in any discussion of ophidian phylogeny, which, in the absence of paleontological data, must mainly be based on the structure and development of living forms. Camp (1923) suggested that the snakes were derived from forms related both to the fossil mosasaurs and to the varanid lizards*. This observation was based on certain resemblances shown by the cranial anatomy of snakes and varanids (the presence of a long retractile tongue, frontal downgrowths encircling the olfactory lobes), and on similarities exhibited by other structures: vertebrae, hemipenes.

A comparison between certain features of the cranial anatomy of snakes and varanids has been given elsewhere (Bellairs, 1949b), but certain criticisms of Camp's view may be advanced here. The long retractile tongue of varanids, together with the vomeronasal organs with which it is functionally associated, undoubtedly resemble the corresponding ophidian structures. A tongue of similar appearance, however, is found in the teiid lizard *Tupinambis*, and the vomeronasal organs of amphisbaenids are very like those in snakes. The presence of frontal downgrowths has been described in many lizards besides *Varanus*, and is of ambiguous phylogenetic significance. The endocranial brain-case of *Varanus* (fig. 3) is typically saurian; the interorbital septum is well developed and the lateral cartilages, though less extensive than in *Lacerta*, are better developed than in *Anguis*, *Anniella* or *Acontias*. Finally, the retractor bulbi group of eye muscles is well developed in *Varanus*, and as in *Lygosoma* (see fig. 2) extends far back into the deep hypophyseal fossa (Säve-Sodebergh, 1946). In snakes this group of muscles appears to be absent, and the hypophyseal fossa is relatively shallow.

Since the varanids have been shown to bear little significant resemblance to snakes in so far as the structures considered in this investigation are concerned, it seems desirable to examine conditions in other groups of lizards. Such examination suggests that those forms whose cranial osteology most nearly resembles that of snakes are the specialized burrowing lizards such as *Acontias*, *Nessia* and *Anniella*. These lizards exhibit a number of striking similarities with burrowing snakes, so that Brock (1941) has observed that 'The burrowing lizards and burrowing snakes form an intermediate series which completely bridge the gap between the typical lizards and specialized snakes'. While it is clear that the features considered are of adaptive significance their occurrence even in surface-living snakes is also suggestive of a true phylogentic affinity. Such a possibility was envisaged by Brock in her study of the skull of

* In his classification, Camp (1923) splits the Suborder Sauria into two main Divisions, the Ascalabota and the Autarchoglossa. The latter contains the section Anguimorpha, a group which includes the Platynota, comprising the Superfamilies Varanoidea (Varanidae and some extinct relatives, Aigialosauridae and Dolichosauridae) and Mosasauroidea. Camp stresses the affinities of the Serpentes with the Anguimorpha in general, and suggests a particular relationship with the Platynota. He states (p. 359) 'I cannot regard the Serpentes as anything but highly modified anguimorphine lizards near the platynotid stock'. In his phylogenetic chart (p. 333) he shows the snakes as derived from a branch of the same stem as gave rise to the varanids and other platynotids, the precise relationship between Serpentes and Platynota being indicated as uncertain. This concept is expressed more emphatically by Romer (1945, p. 208) who writes that the snakes were 'Obviously derived from varanid types'. The criticisms given above do not apply to the assumption of a general relationship between the snakes and the Anguimorpha, but only to the view that the former have specially close affinities with the Varanidae.

Acontias. She suggests that apart from the modification of the jaws in snakes, the remaining characteristics of the ophidian skull such as the cranial box formed from the frontal and parietal downgrowths, the width of the orbito-temporal region and the absence of the temporal arcades are all associated with a subterranean existence.

Comparison between a burrowing lizard such as *Anniella* (fig. 1 B) and a burrowing snake such as *Typhlops* (fig. 1 D) suggests certain evolutionary possibilities. A continued diminution of the size of the eyes beyond that in *Anniella*, associated with loss of the orbital cartilages, a further reduction in the height of the trabecular part of the interorbital septum and an increase in the extent of the paired parts of the trabeculae at the expense of the trabecula communis, would result in a condition not unlike that of *Typhlops*.* Such a tendency has apparently occurred in *Acontias* where the interorbital septum is lower and the orbital cartilages have been even further reduced than in *Anniella*. *Acontias* also shows a closer approximation to the ophidian condition in that downgrowths from the parietals, as well as from the frontals, are described by Brock. These downgrowths must have been developed at some period during the evolution of snakes, and although their presence is not restricted to burrowing forms it has been shown to be characteristic of them. At all events, this feature could be interpreted equally well as evidence for the derivation of snakes from a burrowing ancestor as from a typical member of the surface-living genus *Varanus*.

Conditions in the Amphisbaenidae deserve mention in this context. The general disposition and relationships of the eyes, cranial cavity and trabeculae resemble those in burrowing snakes, and these forms might be adduced as representing a transitional stage between burrowing lizards such as *Acontias* and burrowing snakes. The presence of ossified endocranial side-walls and the extra-cranial course of the ophthalmic nerves, however, alone show that the amphisbaenids could have had no place in the direct line of ophidian phylogeny. They can perhaps be regarded as a group which has independently approached the ophidian type of organization in many ways.

The possible course of evolution previously outlined is in accordance with the views expressed by Brock (1941) and Mahendra (1938) who regards the Leptotyphlopidae and Typhlopidae as being nearer to the ancestors of snakes than any other living forms. Both these workers based their conclusions largely on features exhibited by the ossified skeleton. A more vigorous exposition of the theory that the snakes were derived from burrowing ancestors has been advanced on other grounds by Walls (1942, etc.) who apparently reached this conclusion without reference to the work previously cited. This view has previously been discussed by Bellairs and Boyd (1947) and need not be recapitulated at length here. Wall's theory presupposes some degree of reversibility of evolution. He postulates that the snakes were derived from ancestors in which the eyes had undergone marked degeneration in association with burrowing habits. He suggests that after thorough adaptation to fossorial life had occurred the majority of snakes emerged from their subterranean habitat and succeeded in establishing themselves in a variety of ecological situations above ground. Their eyes became re-enlarged and regained a high degree of functional efficiency, but they still retain evidences of their erstwhile degeneracy; notably the brille or spectacle, and a number of peculiarities of their intrinsic elements. The explanation of these features involves assumption of reversibility of evolution in some, but not in all cases. The loss of the retractor bulbi musculature might be regarded as additional evidence for Walls' view.

* Burrowing specializations have been evolved independently by members of several saurian and ophidian families. It is not suggested that the Scincidae and Anniellidae were necessarily near the line of evolution to snakes, nor that the Typhlopidae represent the ancestral group from which other snakes have been derived. The forms cited, however, are probably more specialized for burrowing life than any others of which the chondrocranium is known. They have, therefore, been used as examples to illustrate an evolutionary trend which might conceivably have taken place.

The course of evolution outlined might provide some explanation for the platytraby of snakes, but it would be necessary to assume that the reversible changes were confined to the eyes and did not affect the skeleton. Once a condition like that in *Typhlops* had been reached where the interorbital septum had been reduced to a trabecula communis, a slight increase in eye size unaccompanied by any change in the level of trabecular fusion would result in the typical ophidian state where the chondrocranium is platytrabic at mid-orbital level. This condition is present in *Rhinophis* (fig. 9G–J), a form only slightly less adapted to burrowing life than *Typhlops*.

The implications of such a theory may be stressed. It would be necessary to suppose that many of the burrowing specializations described in a form like *Typlops* constitute features which are actually primitive for the whole order Serpentes. This view, with its assumption of orthogenesis for certain characters associated with reversibility of evolution in the case of some others is difficult to accept without further evidence. On the basis of the characters considered in this paper alone, however, it provides at least a plausible account of ophidian phylogeny. The origin of snakes can only be determined with any certainty by paleontological findings.

In the absence of such data, the theory that the snakes have been derived from burrowing ancestors deserves serious consideration. Such consideration should, however, be based on a far wider range of morphological characters than have been studied in this paper.

Summary.

1. The anterior brain-case is defined as that part of the skull formed by cartilage or bone, which lies between the nasal capsule in front, and the basal plate and otic capsule behind. In all tetrapods this includes both membrane bones and endocranial elements; the embryological components of the latter are described, and an account of the platytrabic and tropitrabic types of chondrocrania is given.

2. The morphology of this region throughout the tetrapod series is briefly reviewed. In primitive forms such as the early embolomerous labyrinthodonts, the endocranial parts of the anterior brain-case were ossified, and conformed to the tropitrabic type with an interorbital septum. In some groups including the modern amphibia this ossification was reduced and the brain-case also became platytrabic.

3. The endocranial ossifications of the anterior brain-case were reduced at an early stage in the evolution of most groups of reptiles. This trend has been most marked in the Squamata, and is least apparent in the amphisbaenids, and in the archosaurs and their avian descendants. In some forms compensation for this endocranial reduction was provided by downgrowths from the frontals and parietals.

4. In most modern reptiles the tropitrabic type of chondrocranium has been retained, and an interorbital septum is present.

5. The ontogenetic development of the interorbital septum from the trabeculae and other structures has been investigated in reptiles. At an early stage in ontogeny the trabeculae are paired in all forms. In Sauria, Rhynchocephalia and Crocodilia these structures fuse later to form a trabecula communis. In most Testudines the trabeculae fuse with a median bar of cartilage, the intertrabecula, which develops in the mesenchymatous tissue between them. The trabecula communis or (in turtles) the trabeculae and intertrabecula then fuse with the medial parts of the orbital cartilages to form the interorbital septum. In *Sphenodon* and lizards the septum subsequently undergoes secondary fenestration.

6. In snakes and amphisbaenids conditions differ from those in other living reptiles. In adult snakes the brain-case in the orbital region consists only of the trabeculae which remain paired at this level. Structures regarded as rudimentary orbital cartilages are described, however, in snake embryos. In Amphisbaenidae the trabeculae fuse but no true interorbital septum is present. A provisional interpretation of the lateral elements of the amphisbaenid endocranium is given. These elements are well ossified, and this feature would seem to warrant a more distinct taxonomic status for the group.

7. The characteristics of the brain-case in Squamata are considered with special reference to their bearing on the origin of snakes. Certain differences in the cranial morphology of varanids and snakes are discussed, and it is suggested that a varanid origin of snakes should not yet be regarded as certainly established. The possibility that the snakes might have been derived from burrowing ancestors is discussed.

I am grateful to Prof. J. D. Boyd for his helpful criticism and continued interest in this work.

Reptilian Genera Examined.

Serial sections through the orbital region of members of the following genera were available. Unless otherwise indicated, each generic name refers to a single post-natal specimen. Where more than one specimen was examined, the number is shown in brackets after the generic name. Embryonic stages showing the chondrocranium are indicated by the letter E after the generic name ; the number of successive stages examined is also shown.

Rhynchocephalia	*Sphenodon* (4 E). (Dendy Collection).	
Testudines	*Testudo*, *Caretta* (1 E), *Chrysemys* (1 E), *Chelydra* (4 E).	
Crocodilia.....	*Crocodilus* (1 E), *Alligator* (3 E).	
Sauria.....	Varanidae.	*Varanus* (2).
	Lacertidae.	*Lacerta* (2), *Lacerta* (10 E).
	Anguidae.	*Anguis* (2), *Anguis* (12 E).
	Agamidae.	*Calotes* (4 E), *Agama*.
	Iguanidae.	*Anolis*.
	Geckonidae.	*Hemidactylus* (2), *Hemidactylus* (3 E).
	Tarentola, *Stenodactylus*, *Ptenopus*, *Coleonyx*, *Cnemaspis*.	
	Rhiptoglossa.	*Chamaeleo* (2 E).
	Scincidae.	*Chalcides*, *Chalcides* (1 E), *Mabuia*, *Nessia*.
	Anniellidae.	*Anniella* (2).
	Pygopodidae.	*Lialis* (2).
Amphisbaenidae.....	*Amphisbaena*, *Trogonophis* (2), *Rhineura*.	
Serpentes	Typhlopidae.	*Typhlops* (2), *Typhlops* (1 E).
	Anilidae.	*Cylindrophis* (2).
	Uropeltidae.	*Rhinophis*.
	Xenopeltidae.	*Xenopeltis*.
	Boidae.	*Constrictor*, *Python* (2 E), *Trachyboa* (1 E), *Eryx*.
	Colubridae.	*Natrix*, *Natrix* (4 E), *Thamnophis*, *Elaphe* (1 E), *Homalopsis* (1 E), *Bungarus*, *Thamnophis* (1 E).
	Viperidae.	*Bitis* (1 E), *Vipera* (2), *Vipera* (6 E).

Addendum.

Since this paper has gone to press, sections through the heads of the iguanid lizard *Anolis equestris* and the amphisbaenid *Rhineura floridana* have become available. In *Anolis* the wings of the planum supraseptale extend dorsally around the long slender olfactory lobes, so that the latter are more completely enclosed by cartilage than in most other lizards. The posterior part of the planum and the pila metoptica are very massive, and the latter are partly ossified. In *Rhineura* the condition of the orbitosphenoids is very similar to that in the other amphisbaenids described, but the trabecula communis is ossified forwards to the ethmoidal region, and is fused with the orbitosphenoids.

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ABBREVIATIONS TO FIGURES AND PLATES.

add.m.	adductor mandibulae muscle.
a.pr.bs.	anterior process of basisphenoid.
b.c.f.	basicranial fenestra.
bs.	basisphenoid.
btp.	basitrabecular process of basisphenoid.
car.f.	foramen for internal carotid artery.
c.hyp.	cartilago hypochiasmata.
cond.	ectomeningeal condensation.
con.s.	conjunctival space.
d.J.o.	duct of Jacobson's organ.
d.n.p.	ductus nasopharyngeus.
do.s.	dorsum sellae.
du.	dura mater.
ec.c.	ectochoanal cartilage.
ecpt.	ectopterygoid.
*f.*1, 2, 3.	fenestrae 1, 2, 3 in interorbital septum.
fb.	forebrain.
f.olf.	fenestra olfactoria.
fr.	frontal.
fr'.	frontal downgrowth.
Hd.gl.	Harderian gland.
hyp.	hypophyseal fossa.
i.o.b.	inferior oblique muscle and attachment.

Abbreviation to Figures and Plates (*cont.*).

i.o.s.	interorbital septum.
i.r.	inferior rectus muscle and attachment.
itr.	intertrabecula.
J.o.	Jacobson's organ.
ju.	jugal.
la.d.	lachrymal duct.
la.gl.	lachrymal gland.
las.	laterosphenoid.
l.r, l.r'.	lateral rectus muscle and attachments.
M.c.	Meckel's cartilage.
men.	basitrabecular meniscus cartilage.
m.r, m.r'.	medial rectus muscle and attachments.
mx.	maxilla.
na.	nasal.
na.cap.	nasal capsule.
na.s.	nasal septum.
olf.b.	olfactory bulb.
or.c.	orbital cartilage.
ors.	orbitosphenoid (ossified pila metoptica).
ot.cap.	otic capsule.
pabs.	parabasisphenoid.
p.ac.	pila accessoria.
pal.	palatine.
p.ant.	pila antotica.
par.	parietal.
pas.	parasphenoid.
pas.r.	parasphenoid rostrum.
p.met.	pila metoptica.
p.m.p.	processus maxillaris posterior.
pmx.	premaxilla.
pn.w.	postnasal wall (planum antorbitale).
po.	postorbital
p.o.p.	preoptic pillar.
prfr.	prefrontal.
pro.	prootic.
p.ss.	planum supraseptale.
pt.	pterygoid.
ptfr.	postfrontal.
retr.b.	retractor bulbi muscle and attachment.
s.b.s.	sub-brillar space (closed conjunctival space).
sc.	sclera.
sc.c.	sceral cartilage.
s.inf.	subiculum infundibuli.
sl.gl.	superior labial gland.
smx.	septomaxilla.
s.ob.	superior oblique muscle and attachment.
sph.c.	sphenethmoid commissure.
s.r.	superior rectus muscle and attachment.
t.mar.	taenia marginalis.
t.med.	taenia medialis.
tr.	trabecula.
tr.c.	trabecula communis.
vo.	vomer.
I.	olfactory nerve.
V.	vomeronasal nerve.
II.	optic nerve and foramen.
IV.	trochlear nerve and foramen.
V.	trigeminal nerve and foramen.
Va.l.	lateral ethmoidal branch of *Va*, ophthalmic nerve.
Va.m.	medial ethmoidal branch of *Va*.
VII.pal.	palatine branch of VII, facial nerve.

EXPLANATION OF THE PLATES.

Plate 9.

A–D. *Anguis fragilis*. Transverse sections through mid-orbital region of successive embryonic stages showing development of interorbital septum and orbital cartilages. All sections stained with Ehrlich's haematoxylin and eosin.

A. *Anguis* embryo, c. 3·3 mm. head-length. Procartilaginous trabeculae still recognizable as paired structures. Ectomeningeal condensation present at sides of brain. (c. × 56.)

B. *Anguis* embryo, c. 3·5 mm. *h*–1. Trabeculae more closely fused. Ectomeningeal condensation extending downwards away from dura to reach trabeculae. (c. × 67.)

C. *Anguis* embryo, c. 3·8 mm. *h*–1. Fused trabeculae becoming cartilaginous. Ectomeningeal condensation now procartilaginous and downturned medial edges joined with trabeculae (c. × 64.)

D. *Anguis* embryo, c. 4·2 mm. *h*–1. Orbital cartilages now chondrified and fused with trabecula communis to form unfenestrated interorbital septum. Medial edges of orbital cartilages still not completely fused with each other.

Plate 10.

A. *Anguis* embryo, c. 4·5 mm. *h*–1. Appearance of fenestra 3 by absorption of cartilage at region where orbital cartilages join trabecula communis. (Ehrlich's haematoxylin and eosin, c. × 53.)

B. *Anguis* embryo, c. 5·2 mm. *h*–1. Orbital cartilages now form the planum supraseptale of adult morphology. Fenestra 3 more extensive. (Masson's trichrome, c. × 53.) Reconstruction of chondrocranium shown in fig. 6 A (c. × 60.)

C. *Natrix natrix* embryo, c. 8 mm. *h*–1. Transverse section through mid-orbital region. Ectomeningeal condensation takes the form of a septum in the midline dorsal to the trabeculae. Rectangle outlined corresponds with area shown in E. (Heidenhain's haematoxylin and eosin, c. × 47.)

D. *Lacerta vivipara*, embryo, c. 2·5 mm. *h*–1. Transverse section through mid-orbital region. Trabeculae still paired. (Ehrlich's haematoxylin and eosin, c. × 59.)

E. *Python molurus*, embryo, c. 12 mm. *h*–1. Transverse section through trabeculae corresponding with area in inset square in C (*Natrix*). Small nodule of cartilage visible in mid-line dorsal to trabeculae. (Masson's trichrome, c. × 84.)

Plate 11.

A–D. *Chelydra serpentina*. Transverse sections through mid-orbital region in successive embryonic stages showing formation of interorbital septum from trabeculae, intertrabecula and orbital cartilages. A, C and D stained with Ehrlich's haematoxylin and eosin, B with Heidenhain's haematoxylin and eosin.

A. *Chelydra* embryo, c. 5·5 mm. *h*–l ; 7 mm. carapace-length. Wedge-shaped intertrabecula sandwiched between trabeculae which are continuous above with orbital cartilages. Skeleton is mainly procartilaginous. (c. ×45.)

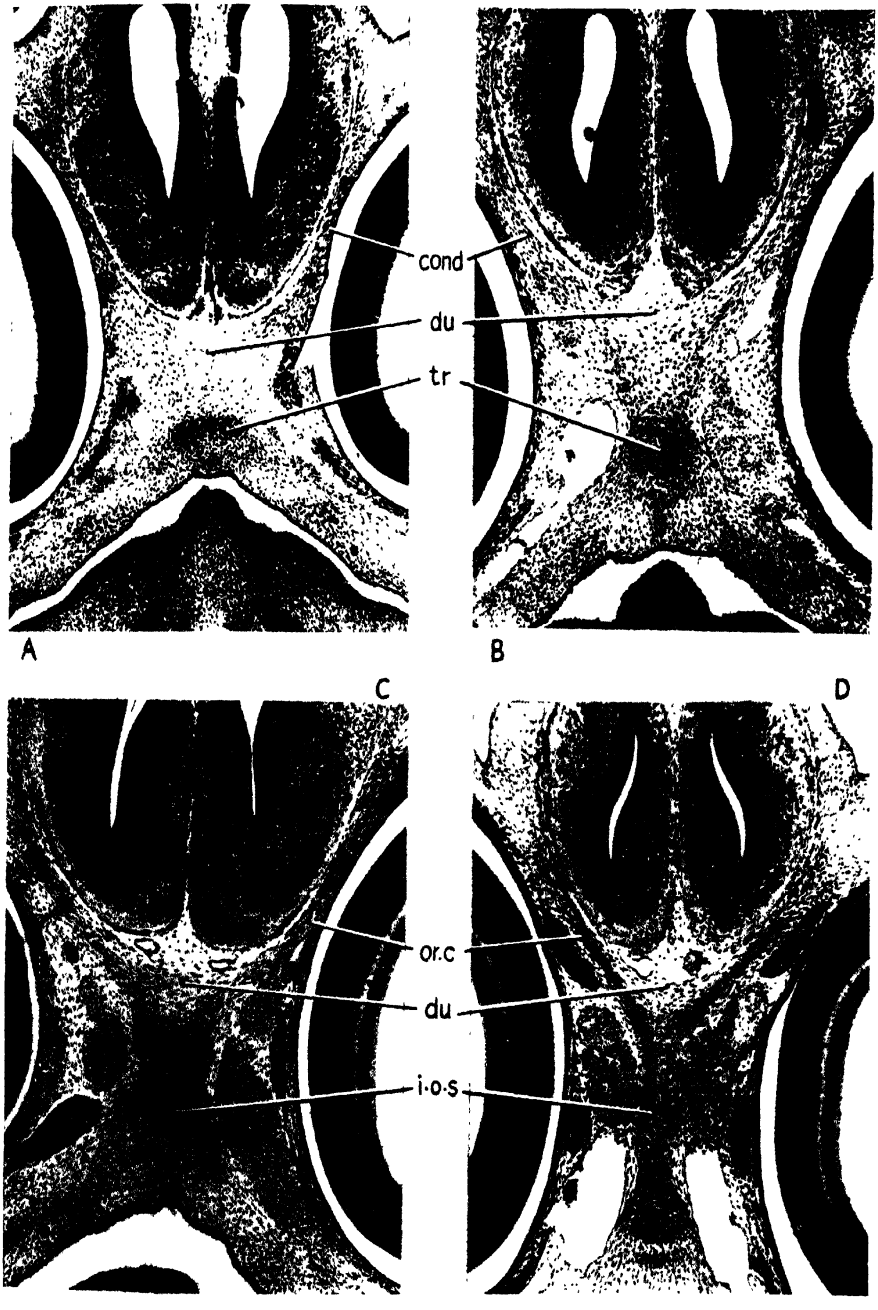
B. *Chelydra* embryo, c. 6 mm. *h*–l ; 7 mm. c–l. Trabeculae are still visible on either side of intertrabecula. (c. ×57.)

C. *Chelydra* embryo, c. 9 mm. *h*–l ; 11 mm. c-l. Trabeculae, intertrabecula and orbital cartilages are no longer visible as separate structures. (c. ×54.)

D. *Chelydra* embryo, c. 10 mm. *h*–l ; 14·5 mm. c-l. Reconstruction of chondrocranium shown in fig. 6 B. (c. ×60.)

Lettering to Plates.

c., nodule of cartilage in python embryo. *cond.*, ectomeningeal condensation. *du.*, dura. *f.*3, fenestra 3 in interorbital septum. *i.o.s.*, interorbital septum. *i.o.s'.* part of *i.o.s.*, derived from fused trabeculae. *itr.*, intertrabecula. *or.c.*, orbital cartilage. *p.ss.*, planum supra-septale. *tr.*, trabecula.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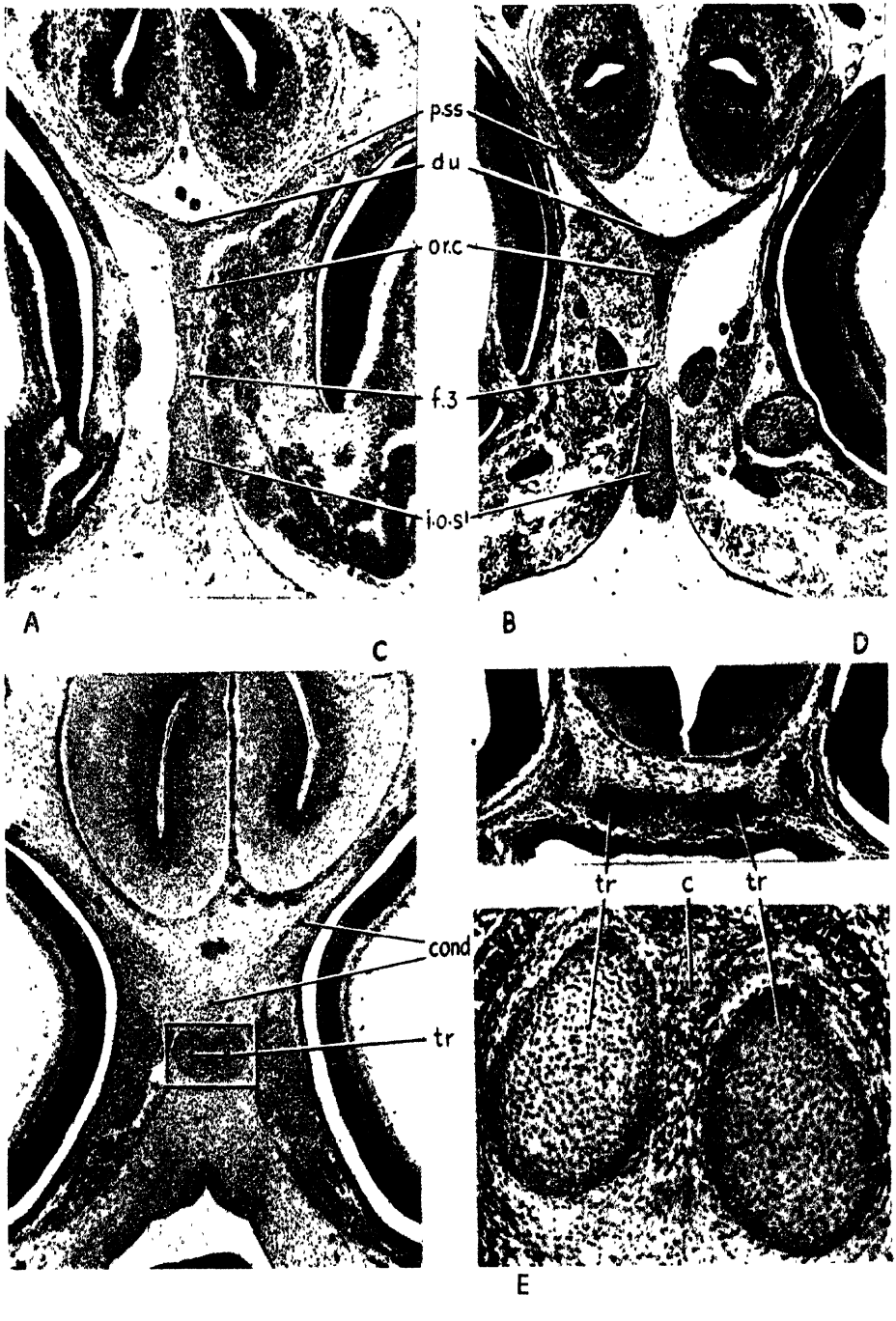
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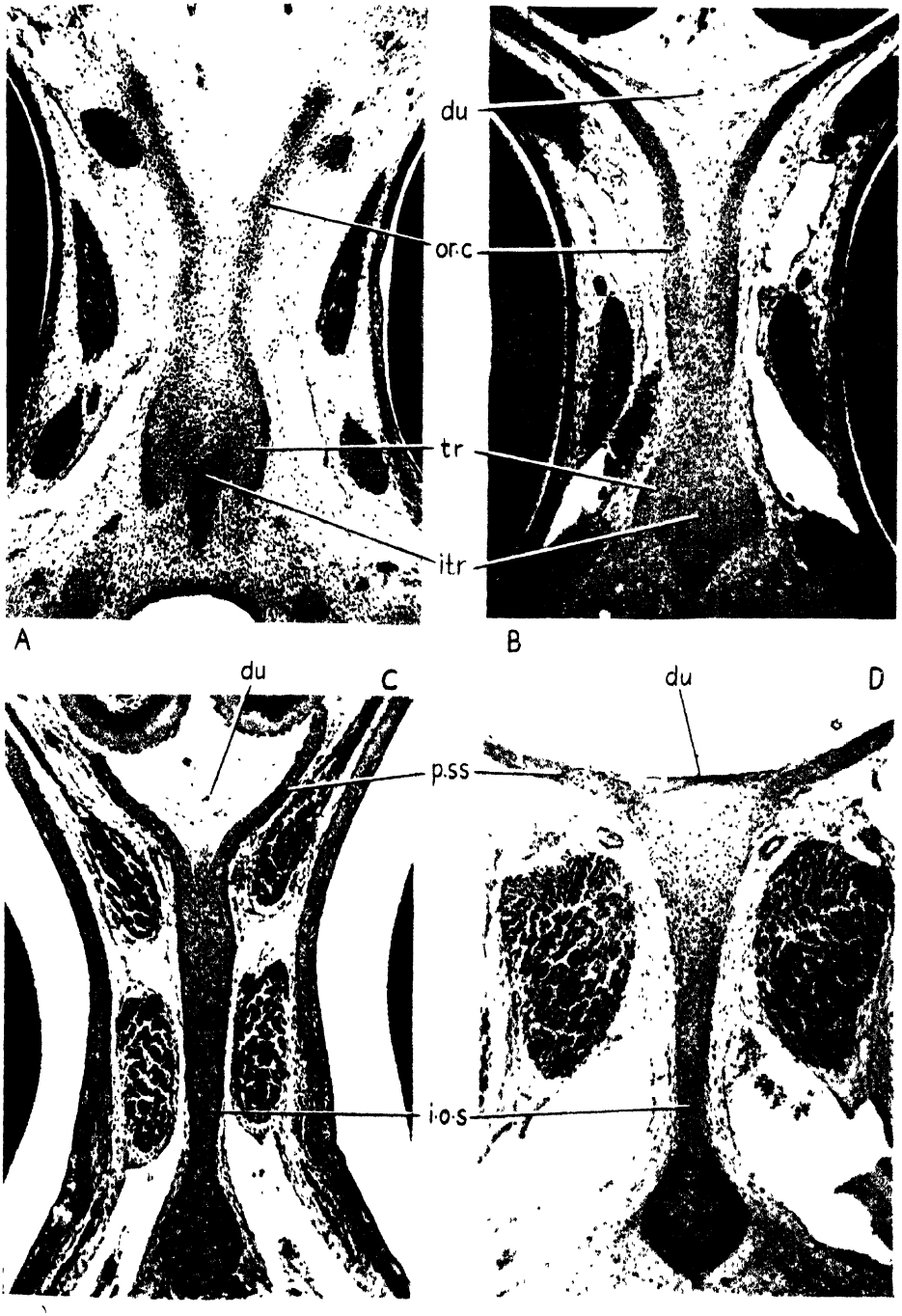
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On the Polyzoan Genus *Hippomenella* Canu & Bassler and its Genotype *Lepralia mucronelliformis* Waters.

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(With 2 Text-figures.)

[Read 10 March 1949.]

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I. Introduction.

During my researches into the Tertiary Polyzoa of New Zealand, the status of certain genera of the Ascophora came under review, including *Hippomenella* Canu & Bassler (1917, p. 41). As there has been much confusion about the true nature of this genus, I am re-describing the genotype, re-defining the genus, and discussing briefly the various species which have been placed in *Hippomenella* by earlier writers.

II. Acknowledgments.

My grateful thanks are due to Canon J. de C. Barreto, Curator of the Museu do Seminario da Incarnação, Funchal, Madeira, for lending the lectotype of *H. mucronelliformis*, and for providing additional material which revealed the nature of the fertile zooecia for the first time; to Dr. J. B. Panouse of the Institut Chérifien, Rabat, Morocco, for the loan of material identified by Canu & Bassler (1925, p. 30); to Dr. P. M. Butler of Manchester University for information regarding the genotype; to the Keepers of the Departments of Zoology and Geology in the British Museum (Natural History) for the facilities given to me for studying the collections; and to Dr. Anna B. Hastings and Dr. H. Dighton Thomas of those respective Departments for their helpful criticism of my work.

III. Hippomenella mucronelliformis (Waters).

1899. *Lepralia mucronelliformis* Waters, p. 11, pl. 3, figs. 15, 21.
1909. *Lepralia mucronelliformis* Waters: Norman, p. 306.
1917. *Hippomenella mucronelliformis* (Waters) Canu & Bassler, p. 42.
1920. *Hippomenella mucronelliformis* (Waters): Canu & Bassler, p. 380, text-figs. 116 A, B.
1925. *Hippomenella mucronelliformis* (Waters): Canu & Bassler, p. 30.
1928. *Lepralia mucronelliformis* Waters: Canu & Bassler, p. 108.
1938. *Hippomenella mucronelliformis* (Waters): Marcus, p. 223.

Lectotype (chosen by Norman, 1909, p. 306):—J. Yate Johnston Collection, Museu do Seminario da Incarnação, Funchal, Madeira. One unnumbered specimen encrusting a lamellibranch fragment, 9·5 × 5 mm.

Other Material:—Madeira, one specimen encrusting a lamellibranch fragment on slide labelled '*Lepralia mucronelliformis* Waters' by Waters — ? part of original material (Waters Collection, Manchester Museum); 1947.4.14.1 *, Madeira, one specimen encrusting a lamellibranch fragment along with *Escharina pes-anseris* (Smitt) and *Tubulipora* sp. (Norman Collection); 1947.8.12.1, Madeira, one specimen

* Specimens in the British Museum (Natural History) are referred to by their Register Numbers.

encrusting a lamellibranch shell (presented by Canon J. de G. Barreto) ; Coast of Morocco (' Vanneau ' Stn. XI, Lat. 09° 33′ W., Long. 32° 32′ N., in 110 metres), one specimen encrusting a pebble (Institut Chérifien, Rabat, Morocco).

DIAGNOSIS :—Zoarium encrusting. Orifice oblong with small rounded and proximally-directed condyles, its proximal end partially covered by a rounded mucronate tubercle. Peristome thickened and distinctly raised bearing six or seven stout tubular spines. Central part of frontal wall smooth or covered with small rounded tubercles, the outer margins of the frontal wall perforated by concentric rows of tubular pores. Frontal avicularia usually paired, one often much larger than the other, mounted irregularly near the edge of the zooecium, the sharply pointed mandibles directed

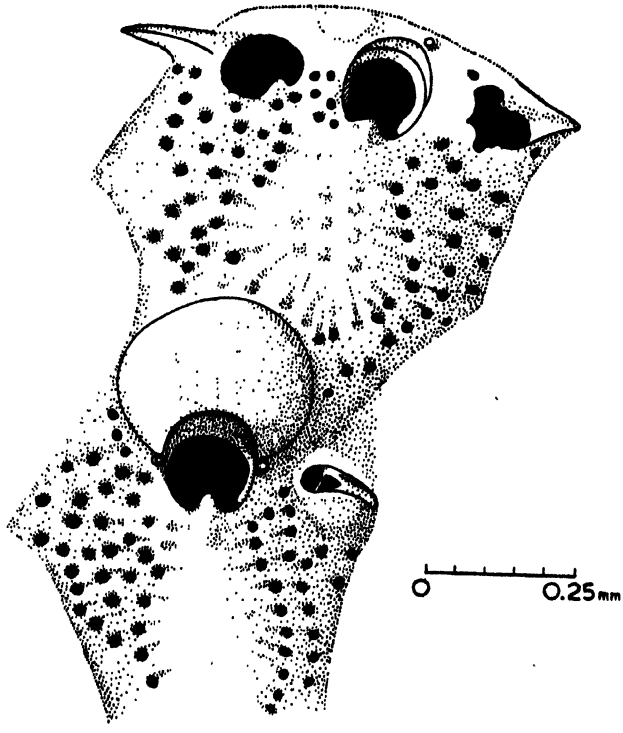

FIG. 1.—*Hippomenella mucronelliformis* (Waters). Madeira, 1947.4.14.1. Two zooecia, the lower with an ovicell. The paired avicularia of the upper zooecium are broken.

outwards or proximally. Ovicell hyperstomial, globular, finely perforated, scarcely ornamented, not immersed in the distal zooecium.

DESCRIPTION :—*Zoarium* encrusting.

Zooecia large, ventricose, somewhat hexagonal in outline, arranged in diverging rows, distinctly separated by deep furrows. *Orifice* oblong, semicircular distally, with a pair of small rounded lateral condyles placed deeply in the peristomie near the proximal end and directed proximally, the poster shallow and of approximately the same width as the anter. Proximal margin straight and covered by a prominent rounded tubercle or mucro directed distally. *Vestibular arch* rather prominent. *Operculum* strongly chitinized with a thick marginal sclerite bearing a pair of thickened rounded processes near its proximal ends. *Peristome* thickened and distinctly raised, bearing six or, more usually, seven stout tubular spines, the proximal pair slightly larger. *Frontal wall* broadly convex, with a smooth or lightly tuberculated, imperforate,

subcircular, central area bounded by an external area perforated by a number of widely separated and roughly concentric tubular pores, the perforate area extending round the distal side of the orifice.

Avicularia usually paired, occasionally one only, rarely absent, forming somewhat globular chambers mounted on the frontal wall of the zooecium near the lateral margins at about the level of the orifice. Mandibles heavily chitinized, sharply pointed and distinctly arched, directed outwards or almost proximally, the beak often raised and strongly projecting beyond the margins of the zooecium. Cross-bar thin but complete. Proximal opesia semicircular.

Ovicells hyperstomial, depressed globular, prominent, recumbent on, but not immersed in, the distal zooecium, the frontal wall finely perforated and faintly ornamented with rounded longitudinal ridges. Peristome of fertile zooecia with a pair of stout spines, one on either side proximally to the ovicell. Orifice of the ovicell closed by the zooecial operculum.

Ancestrula similar to other zooecia but markedly smaller, its paired avicularia small and placed about half-way along the frontal wall on either side.

Rosette-plates :—Two or three oval multiporous plates in the distal half of each lateral wall.

MEASUREMENTS* :—	L_z=0·65–0·70 mm.	l_z=0·57–0·60 mm.
	h_r=0·10–0·12 mm.	l_r=0·08–0·10 mm.
Ancestrula	L_z=0·46 mm.	l_z=0·29 mm.

REMARKS :—The lectotype, in which none of the individual zooecia has reached old age, retains much of the chitinous integument which tends to mask some of the anatomical features. It is, moreover, without ovicells, as is the specimen in the Waters Collection, Manchester Museum, but the structure of these and of the species as a whole has been made clear by the other specimens mentioned above.

The ancestrula (fig. 2 A) is seen on one edge of the lectotype and, though considerably smaller than the other zooecia, it shows all their characters including six well-developed spines round the distal side of the orifice.

In the first generation the zooecia attain full size, and the avicularia are placed asymmetrically and more distally than in the ancestrula. At about the third generation one of the avicularia may be very large with large chamber, arched mandible, semicircular opesia, and thin cross-bar ; the other is usually small and both are beside the orifice (fig. 2 D). The later zooecia, however, do not always show this contrast between their avicularia, for they may remain approximately equal in size as in the specimen from the Norman Collection, 1947.4 14.1 (fig. 1, upper zooecium). Occasionally the large avicularium is absent, and in one case both avicularia are lacking.

The frontal wall of the zooecium is very curious and distinctive. Waters (1899, pl. 3, fig. 21) depicted the central area as bordered with a row of slit-like radiating pores and described them (p. 11) as ' the end of pore-tubes which pass to the base '. Outside these slits he showed a generally perforate wall, but his figure was very indefinite and an examination of the lectotype, on which that figure was probably based,

* *Note on Zooecial Measurements.*

Measurements of the zooecia of Polyzoa are not of much value since they may vary rapidly from individual to individual in the same colony depending, in encrusting forms, on the type of substratum, etc. Opercular measurements, however, are generally fairly constant in individual species within a limited area of distribution, though scarcely of specific value as Canu & Bassler postulate. As their symbols, ' h_a ' (length of aperture) and ' l_a ' (breadth of aperture) have been used indiscriminately for the apertures and orifices (and sometimes opesiae) of the Anasca and for the orifices of the Ascophora, new symbols, ' h_r ' and ' l_r ' have been here introduced for measurements of the length and breadth of the orifice respectively. In this respect, the following definitions of the structures in question are given :—

Aperture.—The opening occupied by the frontal membrane.

Opesia.—The opening connecting the parts of the body-cavity on the basal and frontal sides of the cryptocyst.

Orifice.—The opening of the tentacle-sheath, generally covered by an operculum in the Cheilostomata.

shows that the chitinous cover masks the outer rows of pores which are, in fact, of the same size and nature as the innermost row of pores, i.e., they are tubes passing obliquely down through the frontal wall. The pores of the innermost row appear rather slit-like, especially in immature zooecia, because incomplete calcification allows an oblique section of the tubes to be seen (fig. 2 E). They are continued

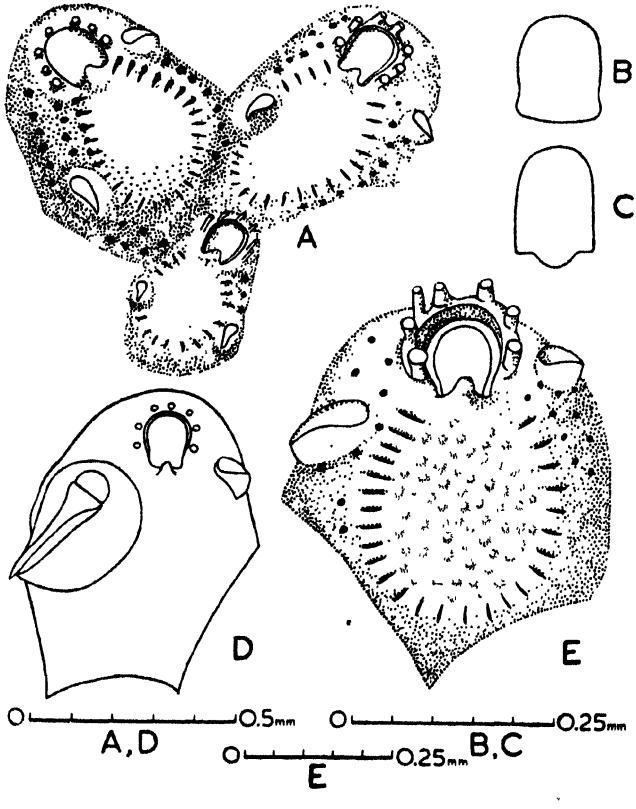

FIG. 2. A, *Hippomenella mucronelliformis* (Waters). Madeira, Lectotype. Three zooecia, including the ancestrula (below). Note the paired sub-equal avicularia on the ancestrula.
B, *H. mucronelliformis* (Waters). Madeira, 1947.8.12.1. Operculum.
C, '*Hippomenella*' *rubra* Canu & Bassler (=*Hippothoa mucronata* Smitt). 'Albatross' Stn. 4205, Gulf of Mexico, 32.3.7.88. Operculum.
D, *Hippomenella mucronelliformis* (Waters). Madeira, Lectotype. Outline drawing of a zooecium to show the large avicularium.
E, *H. mucronelliformis* (Waters). Madeira, Lectotype. Non-ovicelled zooecium with tuberculated frontal wall. The operculum is partially raised and exposes the vestibular arch on the left.

inwards towards the centre of the zooecium as shallow troughs on the frontal wall. Their exact nature is seen in specimen 1947.4.14.1 (Norman Collection) where the troughs have been partially filled in by calcification and remain only as slight furrows radiating across the central area (fig. 1). Dr. Hastings * has remarked on the resemblance of the porous area to an incomplete pleurocyst, the innermost row of pores marking its growing edge. As she herself pointed out, however, there is very little difference in the extent of the porous area in zooecia of different age and no

* Oral communication.

evidence that the central area of the frontal wall ever becomes porous *. If her suggestion is correct, the pores could be regarded as a multiple series of areolae from which the marginal avicularia develop. When the avicularium is very large, its globular chamber tends to spread over the porous wall and overlap on to the central area, and broken avicularian chambers clearly show the underlying pores.

The prominent ovicells are of simple construction and rest upon the frontal wall of the distal zooecium but are not immersed in it. They are of the type found in the family Petraliidae and it is interesting to note that *Lepralia vellicata* Hutton (1873, p. 98) (=*L. rectilineata* Hincks, 1883, p. 201, pl. 7, figs. 5, 5 *a*), which I regard as a *Hippomenella*, has previously been referred to the genus *Petralia*.

Except for the specimen from the coast of Morocco identified by Canu & Bassler (1925, p. 30), which I have examined, the species has not been reported outside Madeira.

IV. The Genus *Hippomenella* Canu & Bassler.

1917. *Hippomenella* Canu & Bassler, p. 41.
1920. *Hippomenella* Canu & Bassler: Canu & Bassler, p. 379.
1930. *Hippomenella* Canu & Bassler: Canu & Lecointre, p. 85.
1935. *Hippomenella* Canu & Bassler: Bassler, p. 127.
? 1940. *Hippomenella* Canu & Bassler: Osburn, p. 430.

Genotype (by original designation):—*Lepralia mucronelliformis* Waters, 1899, p. 11, pl. 3, figs. 15, 21.

The diagnosis of *Hippomenella* given by Canu & Bassler (1917, p. 41) included important characters not found in the genotype, but observed in a number of North American Early Tertiary species which were described later (Canu & Bassler, 1920, pp. 379–393). The most important of these characters concern the ovicell which, although unknown in *L. mucronelliformis* at the time of their observations, was stated to bear 'laterally two areas in the form of a lunar crescent † and more or less perforated', and to be deeply immersed. The ovicell of the genotype is now known not to bear these areas, and to be prominent and not deeply immersed. It is also closed by the zooecial operculum, in contrast to Canu & Bassler's diagnosis.

The genus may now be diagnosed as follows:—Hippoporininae with a finely perforate hyperstomial ovicell. Orifice with a shallow but wide poster separated from the anter by prominent condyles. Frontal avicularia generally paired forming prominent chambers on either side of the median line near the orifice, the mandibles directed outwards. Other subsidiary avicularia may be present. Frontal wall usually with a central smooth imperforate area, often greatly reduced, surrounded by concentric rows of irregular tube-like pores. Oral spines five to seven.

V. Discussion of Species Referred to Hippomenella.

It is very unlikely that *Hippomenella infratelum* Canu & Bassler (1919, p. 92, pl. 6, fig. 2), a vincularian species from the Lower Miocene of Santo Domingo, is correctly referred to *Hippomenella*. Its poster is very narrow and there is a single avicularium placed proximally. Further, an examination of the descriptions and figures of 15 new species ‡ from the North American Early Tertiary sequence placed in this genus by the same authors (1920, pp. 379–393) shows that, with the exception of two, viz. *H. transversata* and *H. angustaedes*, these must be rejected, as their ovicells and often the structure of their frontal walls are very clearly not related to those of

* In *H. vellicata* Hutton sp. (1873, p. 98), a recent New Zealand species, the central area is greatly reduced, though of much wider extent internally, many of the pores in the upper part of the frontal wall not reaching the interior.

† From this character the genus takes its name.

‡ Four of these species, *H. radicata* (D.34658), *H. rotula* (D. 34637), *H. crassicollis* (D. 34675), and *H. capitimortis* (D. 37321), are represented in the Geological Department by material named and sent by Dr. Bassler. They should probably be referred to the genus *Hippopleurifera* Canu.

the genotype*. Complete ovicells are not known in either of the species named but the appearance of their frontal walls suggests that they belong to *Hippomenella*.

In the same work (p. 380), Canu & Bassler included an Australian species, *Mucronella perforata* Maplestone, 1902, in *Hippomenella*. I am unable to discover this in Maplestone's published works, but presumably the species referred to is *M. personata* Maplestone (1902, p. 22, pl. 2, fig. 13). Its immersed ovicell is provided with 'a rounded, shallow pit in front of each side of a slightly raised carina', and the species is probably related to the North American species referred to above which I have rejected from *Hippomenella*.

In 1928 Canu & Bassler (p. 108) referred a new species, *Hippomenella rubra*, from the Gulf of Mexico, to this genus stating that it only differed from *Lepralia mucronelliformis* in its 'smaller dimensions, a larger aperture and two more spines on the peristome'; and that *Hippothoa mucronata* Smitt, 1873, was 'very close, perhaps identical'. The species is represented in the British Museum by material (32.3.7.88) from the type-locality ('Albatross' Stn. 4205) named and sent by Dr. Bassler and proves to be quite distinct generically. Its orifice (fig. 2 C—operculum) is schizoporellid with a very broad shallow sinus resembling that of species of *Gigantopora* Ridley, and its frontal wall is bordered by large areolae. The species is, in fact, synonymous with *Hippothoa mucronata* Smitt (1873, p. 45, pl. 8, fig. 169), an identification which Canu & Bassler questioned because their specimens were provided with avicularia whilst Smitt's were unarmed, but their topotype shows clearly that many of the zooecia are without avicularia. Osburn (1940, p. 430) also thought this synonymy probable. His definition of *Hippomenella* and the inclusion in it of *Lepralia fissurata* Canu & Bassler (1928, p. 110, pl. 331, fig. 1), which he figured, further illustrate the unfortunate consequence of the designation of *Lepralia mucronelliformis*, so little known at the time, as the type of the genus.

Two species from the Philippines, named by Canu & Bassler, *Hippomenella repugnans* and *H. porosa* (1929, pp. 323, 324, pl. 38, figs. 1, 1', 2, 3), are also related to some of the North American Early Tertiary species, and have immersed bifenestrate ovicells.

H. parvicapitata Canu & Bassler (1930, p. 19, pl. 2, figs. 7–11, text-figs. 3 A–C), from the Galapagos Islands is represented in the British Museum collections by a topotype (33.12.10.22) and should clearly be referred to *Hippoporina* Neviani as it is closely related to *Cellepora pertusa* Esper sp. (1796, p. 149, pl. 10, figs. 1, 2), the genolectotype of *Hippoporina* chosen by Waters (1918, p. 98). The remarks of Canu & Bassler (1930, p. 20) on the division of *Hippomenella* into two groups, depending on the presence or absence of peristomial mucrones and on the ornamentation of the ovicell, appear to be without foundation.

Of the four species from the Middle Tertiary sequence of Victoria, Australia, referred to *Hippomenella* by Canu & Bassler (1935, pp. 34–36), only one, or perhaps two, seems to be satisfactorily placed in that genus. A topotype of *H. parviporosa* named and sent by Dr. Bassler (D. 33495) differs from *H. mucronelliformis* in its rather more prominent condyles and its more concave poster, but the orifice is essentially of the same nature. The frontal wall is of exactly similar construction and the avicularia, which may number up to four or five, are small and slightly immersed. Ovicells of this species are not known. *H. magna* appears to have the same type of frontal wall as *H. mucronelliformis* but its orifice has a very wide poster. It may belong to *Hippomenella*, but as no specimen of it is available in London, its position remains doubtful. *H. rarirostrata* and *H. vermicularis* must be rejected.

H. mortenseni Marcus (1938, p. 222, text-figs. 21 A–C) from St. Helena is probably not generically related to *H. mucronelliformis*. Its operculum is broader than long, and the poster is narrower than the anter. The frontal wall, moreover, has large marginal areolae while the central area appears to be completely perforate except where the pores are occluded by the frontal tubercles.

* Since this paper went to press my attention has been drawn to a paper by McGuirt in which some of these species are re-described (1941, pp. 75–78).

H. grandirostris Canu & Lecointre (1930, p. 85, pl. 14, fig. 2), from the Faluns of Touraine and Anjou, appears to be correctly placed generically though the authors state that ' Les deux areas de l'ovicelle sont grands, peu profonds, à peine visibles ; la nervure médiane qui les sépare est très peu apparente '.

The figures and description of *H. mitzopoulosi* Kuhn (1936, p. 177, pl. 1, figs. 1 *a*, *b*), from the Miocene of Crete, indicate that it should be rejected from *Hippomenella*. The shape of the orifice and the frontal wall with its single row of marginal areolae are not characteristic of this genus.

As noted above, I regard *Lepralia vellicata* Hutton (1873, p. 98), a recent New Zealand species, as a *Hippomenella*. The central area of its frontal wall is greatly reduced (see Hincks, 1883, pl. 7, fig. 5, as *L. rectilineata*) and, in addition to the paired avicularia alongside the orifice, there may be a large number of subsidiary avicularia on the frontal wall *. The ovicell is hyperstomial but is covered in mature zooecia by a late extension of the frontal wall of the distal zooecium. Another New Zealand species, from the Upper Tertiary beds of Hawkes Bay, described by Waters [1887, p. 60, pl. 7, fig. 16 (non pl. 8, figs. 34–36 = *H. vellicata* Hutton sp.)], is also a species of *Hippomenella*. Details of both these species will be given in my forthcoming work on the Tertiary Cheilostomatous Polyzoa of New Zealand.

VI. Conclusions.

The classification of the Ascophora is still in a chaotic state and much work remains to be done in assessing the characters which may be used to unite various species into generic units. However, there can be no doubt that the structure and shape of the operculum is of prime importance, and there seems no reason to disagree with Canu & Bassler's placing of *Hippomenella* in the sub-family Hippoporininae (Bassler, 1935, p. 33). This unit is based on the characters of the genus *Hippoporina* Neviani, and includes most of the lepralioid Ascophora with the poster separated from the anter by a pair of lateral condyles.

The investigations into *Hippomenella mucronelliformis* have resulted in the rejection of many species from the genus *Hippomenella*, but this work has fortunately coincided with researches by Dr. Hastings into the genus *Hippoplaurifera*, which, she had independently suggested, may embrace many of the rejected species.

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* Twenty-one avicularia, in addition to the paired oral avicularia, were counted on a zooecium of a fossil specimen (D. 36711) from the Castlecliffian CU3 [Upper Pliocene] beds at Castlecliff, Wanganui, New Zealand.

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On the Polyzoan *Cellepora pulchra* Manzoni and the genus *Hippopleurifera*.

By ANNA B. HASTINGS, M.A., Ph.D., British Museum (Nat. Hist.). (Communicated by H. W. PARKER, M.A., F.L.S.)

(PLATES **12** & **13**.)

[Read 10 March 1949.]

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1. INTRODUCTION.

Examination of the recent Mediterranean species *Mucronella soulieri* Calvet shows that it is synonymous with the fossil species which Manzoni had previously named *Cellepora pulchra*, and that it belongs to the genus *Hippopleurifera* Canu.

I am grateful to the Keeper of Geology, British Museum (Natural History), for access to specimens in his Department; to the Keeper of the Manchester Museum for lending me specimens from the Waters Collection; to Mr. W. H. T. Tams for his excellent photographs of a difficult subject; to Dr. D. A. Brown for ready help in various ways including the loan of some very instructive fossil material for comparison of the pleurocyst; and to my husband, Dr. H. Dighton Thomas, for his valuable advice, help and encouragement.

2. HIPPOPLEURIFERA PULCHRA (Manzoni). Pl. **12**, figs. 2–4, Pl. **13**, figs. 1, 1*a*, 2, 2*a*.

Cellepora pulcra [sic] Manzoni (Michelotti MS.), 1870, pp. 336, 338, pl. iv, fig. 20.
Celleporaria pulchra Seguenza, 1880, p. 129.
Lepralia asperrima Reuss, 1874, p. 33, pl. viii, fig. 9.
Mucronella soulieri Calvet, 1902*a*, p. 61, pl. ii, figs. 3, 4; 1902*b*, p. 33; 1906, p. 440.
Lepralia soulieri Waters, 1925, p. 654, pl. xxxvi, figs. 2–4.
Petralia soulieri Barroso, 1925, p. 179, text-figs. 3–5; Stach, 1936, pp. 356, 379.

MATERIAL EXAMINED:—British Museum: Mediterranean, H.M.S. 'Porcupine', 45 fms. (Busk Coll., 99.7.1.1729, 1730, 1731); Mediterranean, McAndrew (Busk Coll., 99.7.1.1732); locality doubtful (Hincks Coll., 99.5.1.828).

Manchester Museum, Waters Coll.: *Recent*: Oran (5 slides, H.1128, two of them from Canu *); Villefranche-sur-mer, S. France (1 slide, H.1128, and 8 unnumbered slides of serial sections). *Fossil*: Miocene? Province of Messina, Sicily (1 unnumbered slide).

* Another slide from M. Canu from Oran in the Waters Collection is labelled in Waters's writing 'see *Lepralia soulieri*'. The specimen has smaller zooecia with marginal areolae and a small median avicularium within the lower lip of the orifice. It appears to be generically distinct from *L. soulieri*.

DISTRIBUTION: Recent: Mediterranean (Busk; Calvet; Waters; Barroso). Fossil: Miocene: Italy (Manzoni; Seguenza); Sicily * (Waters); Austria (Reuss).

DESCRIPTION:—Manzoni's figure gives a very characteristic impression of this species although it is not quite accurate in detail. Six rather widely spaced spines are arranged along the distal two thirds of the rim of the orifice, and there is sometimes a small median, proximal mucro (Pl. **13**, fig. 1). The beaded appearance resulting when only the bases of the spines are present (Pl. **12**, fig. 2) is well represented by Manzoni, except that it does not extend right round the proximal border of the aperture as shown by him.

The fullest description of recent material was given by Barroso, though his figures fail to portray the actual appearance of the species, which is better shown by Calvet. The characteristic sculpture of the fully developed frontal wall, with coarse granulations between the pores (or pits) (Pl. **12**, figs. 2, 4), is best depicted by Manzoni and Reuss. Waters mentioned this feature and (pl. xxxvi, fig. 2) attempted to figure it. The manner of insertion of the spines is inaccurately represented by Barroso. On the other hand I can confirm Barroso's account of the basal wall, the specimens examined by me being hemescharan, or loosely encrusting, and, in those mounted to show the basal surface, having the basal wall rather strongly calcified, with a small oval foramen near the distal end of nearly every zooecium.

Many zooecia are without avicularia. When present the avicularia are usually beside the orifice and directed distally (Pl. **12**, figs. 2, 4). They are rounded or bluntly pointed, and may be long, as figured by Waters and Barroso; or broader, as figured by Manzoni; or much shorter, so that the mandible is little longer than wide (Pl. **13**, fig. 1), as shown by Calvet. The beak may be flat or somewhat raised from the surface of the zooecium. In Waters's specimen from Villefranche the beaks are unusually prominent giving the zoarium a more uneven surface and enhancing the general resemblance to the Petraliidae, discussed below. This is probably, in part at least, because the specimen represents the younger parts of the colony. With increasing calcification the avicularia would presumably have come to be more or less immersed and the difference from other specimens would have gradually diminished.

The ovicell is large, but not prominent, and in Busk's material is covered with coarse granulations and pits like those on the frontal wall (Pl. **12**, figs. 2, 4). In Waters's material there are sometimes fewer, larger, more irregular pits on the ovicell (Pl. **13**, fig. 1); and sometimes only two (Pl. **13**, fig. 1, Pl. **12**, fig. 3). The two proximal spines on each side remain outside the ovicell as shown by Calvet and Barroso. In Waters's material from Villefranche developmental stages of the ovicells can be seen (Pl. **13**, figs. 1, 2, Pl. **12**, fig. 3). In one ovicell whose sides are beginning to curve upwards from the plate on the gymnocyst of the distal zooecium, the distal pair of spines can be seen inside the ovicell *b* (Pl. **13**, fig. 2).

There are obvious discrepancies between the figures of the opercula given by Waters (pl. xxxvi, fig. 3) and Calvet (pl. ii, fig. 4). I have examined Waters's preparation of five opercula and find that his drawing does not correspond to it. In outline the opercula mounted by Waters are very similar to the one in Calvet's figure though the lateral contraction is less marked and is placed more distally. There is no trace of the linear sclerites figured by Waters. On the other hand there is also not exact agreement with Calvet's figure, as I have not seen the muscle dots shown by him. The line on which they lie in Calvet's figure is present in two of the opercula, but is probably not part of the operculum, although it looks like the edge of a thin flange. It is not the inner edge of a wide marginal sclerite, as one might

* Waters gives S. Urbano di Monte Sgrave, N. Italy, in his statement of distribution, but this locality only appears in his discussion in connection with *Lepralia semilaevis* (Reuss) a species which he regarded as distinct from *L. soulieri*. There is no specimen of *L. soulieri* from this locality in his collection, but there is the one from the Province of Messina, which is not mentioned in his paper. This suggests a slip in his statement of distribution.

The Sicilian specimen is labelled 'Rametto, Province of Messina, Sicily, 1876'. Apparently no such place as Rametto exists there, and Dr. Dighton Thomas suggests that the specimen probably came from the Miocene beds at Rometta, west of Messina.

conclude from Calvet's figure. The marginal sclerite is thin and is of fairly uniform thickness on the sides and distal border of the operculum and appears to be absent round the proximal border. The opercula are, however, sufficiently chitinized for Waters to have been able to dissect them out (i.e. they are differentiated, by their thickness, from the membrane forming the floor of the compensation sac). The orifice has been described as without hinge-teeth (cardelles), and this appears to be correct. If, however, one looks obliquely into the orifice of a well preserved specimen with the operculum in position, it is possible to see that the lateral constriction of the operculum is articulated to a very slight thickening of the lateral wall of the orifice which thus functions as if it were a hinge-tooth.

The growing edge is well seen in Waters's specimen from Villefranche (Pl. **13**, figs. 1, 2, Pl. **12**, fig. 3). The calcareous frontal wall appears to grow out above the frontal membrane, the space between the calcareous wall and the membrane becoming the compensation sac, as in *Umbonula littoralis* Hastings, whose development was described by Harmer (*U. verrucosa*, 1902, p. 331). As in *U. littoralis*, the proximal edge of the operculum does not fit closely to the proximal border of the orifice, and, in dried specimens, at any rate, the compensation sac is widely open distally.

The calcareous frontal wall when first formed is smooth or radially striated with small marginal areolar pores in two rows. These two rows of pores can be very clearly seen on the internal surface of the wall in one of Busk's specimens (99.7.1.1731). The secondary calcification spreads from these areolar pores, stages in the process being visible in another of Busk's slides (99.7.1.1732) and in Waters's Villefranche specimen. The secondary calcification forms the characteristic coarse granulations and pits, and transforms the glistening wall of the young zooecium (Pl. **12**, fig. 3, Pl. **13**, fig. 2, and growing edge in Pl. **13**, fig. 1) into the opaque, white wall of the older zooecium (Pl. **12**, figs. 2, 4, and older part in Pl. **13**, fig. 1). When the series of zooecia are separated to expose the lateral walls there is a sharp contrast between the actual lateral wall and the thick layer of frontal pleurocyst surmounting it. The lateral wall is uniform, except for the septula. The pleurocyst is penetrated throughout by the parallel tubules corresponding to the pits at its surface (see 99.7.1.1730). The lateral wall, like the basal wall, is strongly calcified.

Discussion of Synonymy :—Seguenza gave no description of the material that he referred to Manzoni's species, and I have had no opportunity of confirming his record.

Reuss obtained this species from the Miocene of Austria. He gave a more accurate figure of the zooecia than Manzoni's, but did not find avicularia. He described it as new, calling it *Lepralia asperrima*.

Busk recognized the identity of his recent Mediterranean specimens with Manzoni's fossils. His slides are labelled '*Hemeschara pulcra* Manzoni sp.' [sic], and there is a note in his own copy of Manzoni's paper, now in the library of the Department of Geology, British Museum (Nat. Hist.).

Through the kindness of the Manchester Museum I have been able to examine the material identified by Waters as *Lepralia soulieri*. It agrees very closely with Busk's specimens of *Hippopleurifera pulchra*, and, as it is clearly the species described by Calvet, *L. soulieri* becomes a synonym of Manzoni's species.

Waters gave *Mucronella pavonella* Neviani, from the Pliocene and Postpliocene of Italy *, in his synonymy of *Lepralia soulieri*, though in his text he said no more than that the avicularia of Neviani's fossils show 'a connection between *pavonella* and *soulieri*'. Neviani's species is clearly related to *L. soulieri*, and distinct from *Umbonula pavonella* (Alder) †, but I doubt whether they are synonymous. It is possible, but I think very unlikely, that the zooecia with peripheral pores in slit-like depressions, represented in Neviani's figure, show an early stage of the pleurocyst. Unless this is so the species is clearly distinguished from *Hippopleurifera pulchra* (*Lepralia soulieri*) by the sculpture of its frontal wall. Neviani himself regarded his

* *Smittia* (*Mucronella*) *pavonella* Neviani, 1896, p. 44, text-fig. 26; 1901, p. 211, pl. xviii, fig. 11.

† *U. pavonella* (Alder) = *U. arctica* (Sars), see Harmer 1902, p. 332, and Hastings, 1944, p. 282.

Mucronella pavonella as synonymous with *Eschara* (*Hippopleurifera*) *sedgwicki*, which is discussed below, but this identification may also be questioned.

There is a slide of *H. pulchra* in the Hincks Collection (99.5.1.828) labelled in Jelly's writing '*Lepralia robusta* Hincks. Coast of Burmah'. Unfortunately there has been some mistake about the type-specimen of *L. robusta* Hincks (1884, p. 360). Dr. Anderson's Mergui material, on which Hincks based his paper, came to the British Museum in 1885, but the supposed type-slide of *L. robusta* (85.12.29.4) only contains a specimen of *Emballotheca quadrata* (MacG.), a very different species. We have thus to rely on Hincks's description and figure which indicate that *Lepralia robusta* has some features in common with *Hippopleurifera pulchra*, but is probably distinct, the shape of the orifice being the chief distinguishing feature. In the absence of other records of *H. pulchra* in the Indian Ocean, and as there has evidently been some confusion about *Lepralia robusta*, the evidence of Hincks's slide appears doubtful and I have not included Mergui in the distribution of the species.

Waters tentatively included *Umbonula verrucosa* Harmer in the synonymy of this species. I have already discussed (Hastings, 1944, p. 281) Waters's mistake.

REFERENCE TO *Hippopleurifera*:—I refer Manzoni's species to *Hippopleurifera* Canu (1925, p. 764*), the genotype of which is *Eschara sedgwicki* Milne-Edwards from the English Coralline Crag (Pliocene). As noted by Waters (1925, p. 654), *Hippopleurifera pulchra* shows considerable resemblance to the genotype from the English Crag, as described by Busk (1859, p. 67, pl. x, figs. 1*a–d*). I have examined Busk's figured specimens (Geol. Dept. B.M. B.1645), and satisfied myself that they all represent one species, despite Waters's suggestion to the contrary. The figures are very accurate, the zooecia in each figure being recognizable in the specimen (in mirror image) and agreeing in detail. The differences between the figures probably represent different stages of development of the pleurocyst. The variation in the length of the zooecia can be seen in a single colony in another of Busk's specimens (D.3374:3). This specimen has very many ovicells (Pl. **12**, fig. 1). They are usually broader in proportion to their length than those of Busk's figured specimen, which are all broken or incomplete. Their sculpture is rough and irregular, but there is always some tendency to the formation of radial ribs with pits between, and many of the ovicells are definitely radially ribbed. The resemblance of some of the ovicells in Waters's Villefranche specimen of *H. pulchra* to some of those of *H. sedgwicki* is very marked. Moreover, in both species the ovicell overhangs the orifice which thus appears truncated distally in fertile zooecia, unless the ovicell is broken away, when the orifice is seen to be of the same shape as in the non-fertile zooecia. My figures show a marked difference in the prominence of the ovicells, but both species are variable in this respect, and there is no significant difference.

There can be no doubt that *H. pulchra* is congeneric with *H. sedgwicki*. It is, indeed, only distinguished specifically by relatively unimportant differences, namely its smaller and more numerous frontal pores, the absence of the small, frontal avicularium proximal to the orifice which is not uncommonly present in *H. sedgwicki*, and the hemescharan colony, that of *H. sedgwicki* being escharan.

3. HIPPOPLEURIFERA Canu.

A few points about the relationships and systematic position of the genus remain to be considered.

SOME EOCENE AND OLIGOCENE SPECIES:—Brown (1949) has re-examined the type-specimen of *Lepralia mucronelliformis* Waters (1899, p. 11), genotype of *Hippomenella* Canu & Bassler (1917, p. 41), and has also obtained material with ovicells, which were hitherto unknown. He has shown that the majority of the American Eocene and Oligocene species referred to *Hippomenella* by Canu & Bassler (1920, pp. 379–393) appear not to be congeneric with *H. mucronelliformis*; and accepts only two species

* See also Canu & Bassler, 1927, p. 7. In introducing the name in 1925, Canu spelt it *Hippofleurifera*, an obvious misprint.

H. sedgwicki has recently been recorded from several localities in the French Miocene and Pliocene (Julien, 1940, p. 30; Roger & Buge, 1947, p. 227).

(in which the ovicells are not known) as being probably correctly placed in *Hippomenella*, namely *H. transversata* and *H. angustaedes*.

Most of the Lower Tertiary species rejected from *Hippomenella* form a rather homogeneous group. Some of them very much resemble *Hippopleurifera sedgwicki* and *H. pulchra*. For example, *Hippomenella radicata* and *H. tuberosa* Canu & Bassler (1920, pp. 387, 391 ; see also McGuirt, 1941, p. 77) differ chiefly in the orientation of their avicularia which are directed proximally in contrast to the distally directed avicularia of *Hippopleurifera*. The resemblance in the orifice, spines, ovicells and sculpture is very marked, and *Hippomenella radicata* has pores on the basal surface like those of *Hippopleurifera pulchra*. Despite the differences in the avicularia, I refer both these species to *Hippopleurifera*.

The ovicells of the other rejected Lower Tertiary species show a considerable range of variation, but Canu & Bassler's view that they are essentially of one type is supported by the closely parallel variation found within a single species in *Hippopleurifera pulchra*.

I have examined four species which are represented in the Geological Department of the British Museum by material received from the U.S. National Museum. They are : —

(1) *Hippomenella radicata* Canu & Bassler, 1920, Eocene, Jackson, Miss., D.34658.
(2) *Hippomenella crassicollis* Canu & Bassler, 1920, Eocene, Old Factory, 1½ miles above Bainbridge, Ga., D.34675.
(3) *Hippomenella rotula* Canu & Bassler, 1920, Eocene, Jackson, Miss., D.34637.
(4) *Hippomenella capitimortis* Canu & Bassler, 1920, Oligocene, West Bank of Conecuh River, Escambia Co., Alabama, D.37321.

I have already discussed *H. radicata* and referred it to *Hippopleurifera*. There can, I think, be no doubt that the other three are congeneric with it, *H. capitimortis* showing the least close agreement.

I have not seen specimens of the other species described under *Hippomenella* by Canu & Bassler in 1920 and rejected by Brown, but it seems probable that, with few exceptions, they should be transferred to *Hippopleurifera*. The most probable exception is *H. pungens*. The orifice of *Hippomenella* is lepralioid (see Brown), not like that of *Umbonula* (see p. 523 above). This distinction is not easily made on fossil material, but I regard it as more important in separating *Hippomenella* from *Hippopleurifera* than the prominence of the ovicells mentioned by Brown (compare the variation of the ovicells of *Hippopleurifera*, p. 524 above).

Relationship to the Petraliidae:—Barroso (1925, p. 182) noticed the relationship of *Lepralia soulieri* (=*Hippopleurifera pulchra*) to a French Eocene species, *Hippomenella mucronata* (Canu), and Stach (1936, p. 356) indicated some French Eocene species (including *H. mucronata*) and the American Eocene and Oligocene species discussed above as ' probable ancestors ' of the Petraliidae. It is therefore of interest to find that *Hippopleurifera pulchra* is more or less intermediate between the American species, and the Petraliidae, particularly resembling *Hippopetraliella* Stach (1936, p. 369).

Barroso also regarded *Lepralia soulieri* as related to *Lepralia rectilineata* Hincks (1883, p. 201 =*Lepralia vellicata* Hutton, 1873, p. 98). This species has been referred to *Petralia* (*sensu lato*) by Levinsen (1909, pp. 350, 351) *, and to *Hippomenella* by Brown (1949, pp. 517, 519).

Hippopleurifera pulchra differs from the American Lower Tertiary species and resembles *Hippopetraliella* in the secondary calcification of the frontal wall. The secondary calcification of the American species typically takes the form of a granular pleurocyst spreading from one or two rows of marginal areolar pores. In *Hippopleurifera pulchra*, also, the secondary calcification spreads from a double row of

* Levinsen mentioned *P. rectilineata* as an encrusting species, but material in the British Museum is hemescharan (75.1.5.23).

areolar pores, but, instead of being a granular crust, it has a tubular structure, agreeing closely with the frontal wall of the Petraliidae. In the Petraliidae this wall has been described as a tremocyst (Canu & Bassler, 1929, p. 250; Stach, 1936, p. 359), but in *H. pulchra*, where it spreads from marginal pores, it is presumably to be regarded as a pleurocyst (cf. Waters, 1925, p. 655). Canu & Bassler themselves recognized the possibility of including species with both types of wall in a single genus when they described *Hippopleurifera* (*Hippomenella*) *repugnans* (1929, p. 323). This recent species from the Philippines, which closely resembles the Lower Tertiary species, has a complete frontal wall like the frontal wall of *H. pulchra* when the pleurocyst is incomplete.

On the other hand, the ovicell of *H. pulchra* is not finely punctate as it is in all Petraliidae (see Stach, 1936, p. 355), but closely resembles those of some of the Lower Tertiary species (e.g. *Hippopleurifera incondita* (Canu & Bassler), 1920, p. 383, pl. 1, figs. 1–8). The absence of hinge-teeth (cardelles) in *H. pulchra* is perhaps less important since, as shown above, there is a functional articulation of the operculum. The basal (radicular ?) pores are simpler than those of *Hippopetraliella* and resemble those of *Hippopleurifera radicata* (Canu & Bassler, 1920, p. 387, pl. 1, figs. 19–24) one of the American Eocene species which particularly resembles *H. pulchra*. There is no mucro in *Hippopetraliella*, though mucros are common in the Petraliidae.

Comparison with *Umbonula*:—Canu & Bassler (1929, p. 326) compared *Hippopleurifera* to *Umbonula* Hincks (1880, pp. cxxxviii, 316). The specimens represented in Busk's figures *a* and *b* (1859, pl. x, fig. 1) of the genotype, show obvious resemblances to *Umbonula littoralis* Hastings and *U. ovicellata* Hastings (1944) respectively (i.e. to the littoral and deeper-water forms of *U. verrucosa* as understood by Hincks). *

Canu & Bassler described *Hippopleurifera* as differing from *Umbonula* in the presence of hinge-teeth (cardelles), of a strongly chitinized operculum, of lateral avicularia and of rows of interareolar costules. The last of these characters is a point of resemblance, not of difference. The lateral avicularia resemble those of *U. arctica* Sars (see p. 523) in position, and often in shape. The hinge-teeth in Busk's specimens of *Hippopleurifera sedgwicki* are barely discernible, but where best seen are a little more developed than the opercular articulation of *Hippopleurifera pulchra*, *Umbonula* having no trace of articulation of this kind. The characters of the opercula of the fossil genotype of *Hippopleurifera* can obviously only be known in so far as they can be deduced from the characters of the orifice; and the presence of the very minute hinge-teeth hardly warrants the conclusion that the operculum was strongly chitinized. Thus Canu & Bassler's distinctions between *Hippopleurifera* and *Umbonula* amount to no more than the presence of minute hinge-teeth. There is, however, one other difference, namely the presence of spines, which are completely absent in *Umbonula*†.

Systematic Position:—*Umbonula* and *Hippopleurifera* are clearly very closely related. According to the latest classification of Bassler (1935, pp. 32, 33, 34), *Hippopleurifera* is placed in the Hippoporininae, a subfamily of the Escharellidae; *Umbonula* is placed in the Smittinidae; and the Petraliidae are recognized as a distinct family.

I think the best way to express the possible relationships discussed here is to put *Hippopleurifera* and *Umbonula* into one family, and to put this family next to the Petraliidae in the system.

The family Umbonulidae Canu (1904, p. 18) is available for these genera. Canu introduced the family without definition, but with a reference to Harmer 'On the

* For the genotype of *Umbonula* see Hastings, 'Notes on Polyzoa (Bryozoa). iv.' *Ann. Mag. nat. Hist.*, in press.

† As a frequent critic of the details of the work of Canu & Bassler, I should like to put on record my appreciation of their achievements. Their extensive investigations into, and wide knowledge of, the Polyzoa have enabled them to provide a vast store of information and ideas and to build a classification of the whole group, which have given a fresh starting point to us whose work is of more limited scope.

Morphology of the Cheilostomata ' *. The name of the family, and the inclusion in it by Canu only of species referred to *Umbonula*, show that that genus should be taken as the type of the family. On p. 320 of the paper mentioned by Canu, Harmer discussed the taxonomic bearings of his observations, and recognized six types of Cheilostomatous structure. The fifth of these is the ' umbonuloid ' structure described in his detailed account of *Umbonula* in the same paper. This umbonuloid development of the frontal wall is one of the important points relating *Hippopleurifera* and *Umbonula*. Canu's family is thus not only technically appropriate because of its type-genus, but also was evidently intended by Canu for just such an assembly of genera as those discussed here.

It need hardly be pointed out that Harmer's six types of structure represent higher groups than families, and that the genera mentioned as probably having umbonuloid structure are not all to be referred to the Umbonulidae.

4. Summary.

Mucronella soulieri Calvet and *Lepralia asperrima* Reuss are synonymous with *Cellepora pulchra* Manzoni.

Manzoni's species belongs to *Hippopleurifera* Canu, a genus which appears to be related to *Umbonula* Hincks. The two genera may be referred to one family, Umbonulidae Canu, to be placed near the Petraliidae.

Certain American Eocene and Oligocene species, described as belonging to *Hippomenella*, appear to be more nearly related to *Hippopleurifera*. They have been indicated by Stach as possible ancestors of the Petraliidae. *Hippopleurifera* is more or less intermediate in character between these Lower Tertiary species and the Petraliidae as represented by *Hippopetraliella*.

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EXPLANATION OF THE PLATES.

PLATE 12.

Hippopleurifera sedgwicki (Busk) and *H. pulchra* (Manzoni).

FIG. 1. *H. sedgwicki* (Busk).

Part of D.33743, Coralline Crag, [Suffolk], showing ovicells and long and short avicularia. ×c. 60.

FIG. 2. *H. pulchra* (Manzoni).

Part of 99.7.1.1730, showing a complete ovicell (*ov.*) and two broken ovicells. ×c. 60.

av. long avicularium. *sp.* spine bases.

FIG. 3. *H. pulchra* (Manzoni).

Part of the growing edge of the specimen from Villefranche, more highly magnified than in Pl. **13**, showing stages in the development of the pleurocyst. ×c. 100.

ov. 1. smooth ovicell. *ov.* 2. two ovicells with pleurocysts showing foramina. Avicularia also recognizable.

FIG. 4. *H. pulchra* (Manzoni).

Part of 99.7.1.1730 for comparison of the frontal wall with the figures of Manzoni and Reuss. ×c. 100.

PLATE 13.

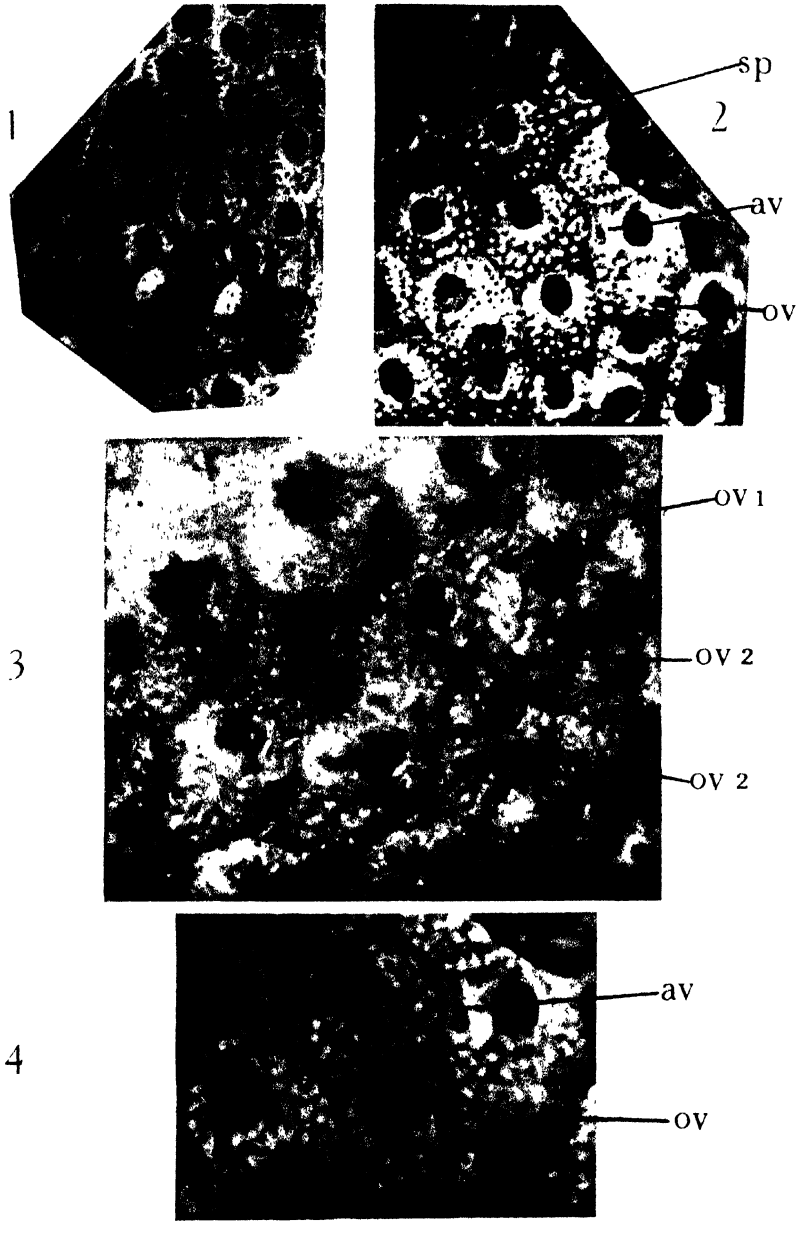
Hippopleurifera pulchra (Manzoni).

FIGS. 1 and 2. Photographs of the growing edge of the specimen from Villefranche showing stages in the development of zooecia and ovicells. ×c. 60.

FIGS. 1 *a* and 2 *a*. Keys to figures 1 and 2.

Zooecium B, with the frontal wall largely membranous, is recognizable in both photographs and shows how they fit together. Zooecia E, F, and G also show clearly in both.

A. incipient zooecium, only proximal end formed, frontal wall membranous. B. zooecium with membranous frontal wall complete, primary calcareous wall (olocyst) beginning to develop over proximal part. C. olocyst nearly complete, note spines. D. olocyst complete, traces of secondary calcification (pleurocyst) appearing at periphery. E, F, G and H. successive stages in development of pleurocyst. *a.* and *b.* successive early stages of ovicell, note spines. *d.* two ovicells complete and smooth. *f.* ovicell with secondary calcification. *g*, *h*, *k*, etc. ovicells with more advanced stages of secondary calcification. *sp.* spines. *anc.* attached cellularine ancestrula.



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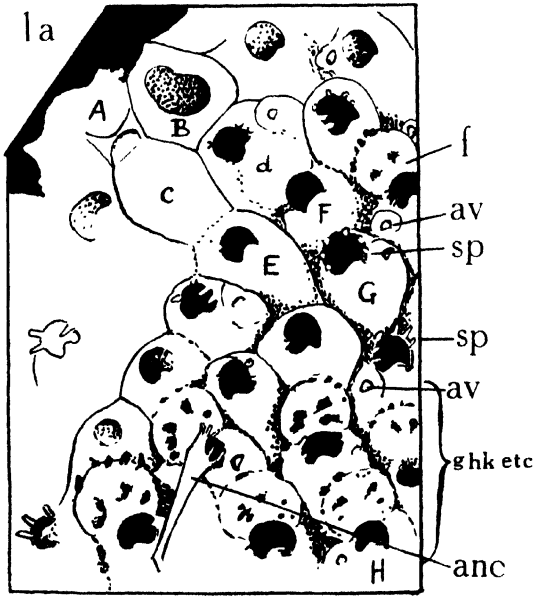

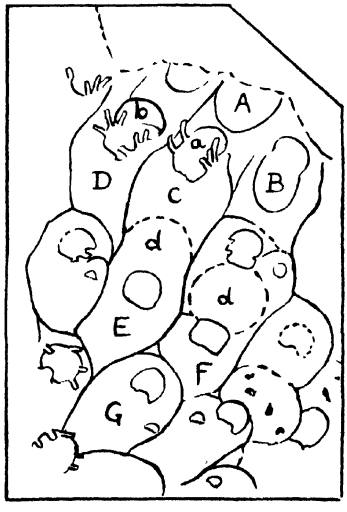

HIPPOPLEURIFERA PULCHRA

The Evolution of Arthropodan Locomotory Mechanisms.—Part I. The Locomotion of Peripatus.

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(PLATES 14–17, and 9 text-figures.)

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INTRODUCTION.

The following account (Part I) presents the results of the first of a series of studies on the locomotory mechanisms of segmented invertebrates which has been undertaken with the object of recording and analysing the normal locomotory movements of a wide range of animals. The data is derived from intact unmutilated specimens progressing under approximately normal conditions. Comparisons of the mechanisms exhibited by animals, both from different groups, and from within the same group, provide clear evidence of the manner of evolution of the various types of gaits, and also gives a functional explanation of the gross body form characterizing these animals. It is further hoped that it may be possible to carry out an analysis of the musculature associated with the several gaits which determines the shape of a segment of the trunk of an animal.

The locomotory mechanism shown by Peripatus provides a key to the understanding of the evolution of the various mechanisms found in higher Arthropoda. (See Part II). The movements of Peripatus are much more varied than they are in terrestrial Arthropoda provided with an exoskeleton. Since an appreciation of both the gaits of Peripatus, and of the principles governing them, are necessary for an understanding of the more advanced Arthropoda, the locomotory mechanism of this animal will be considered below in some detail. The locomotory movements of *Peripatopsis sedgwicki* and of *P. moseleyi* have been investigated by cinematography combined with recording of the footprints.

As long ago as 1889 Haase remarked that photography was needed for the elucidation of the manner of locomotion of Peripatus. Zacker (1933) has given a summary of the literature concerning the locomotion of the Onychophora. Haase (1889) noted the equally effective forward and backward crawling; the absence of conspicuous body movements; the several waves of limb movements which are propagated along the body at one moment; the limbs of a pair being predominantly in phase with one another; and the irregular correspondence of the two sides of the body. He described the general movements of the leg, which usually steps on the sub-terminal pads of spines alone, and only sometimes grips with the paired terminal claws. He recorded a speed of 3·3–4·1 mm. per sec. for an animal 40 mm. long. Some of these

features had been recorded by Moseley (1874). Lankester's observations accompanied by drawings of *P. capensis* (1904) are approximately correct, and he clearly appreciated the need for photography to give data concerning the duration of the forward and backward strokes. Kemp (1914) makes brief reference to different types of locomotion in Peripatus but he does not define the gaits.

Movements of the Head.

The cinematograph records show that the head end of the body, particularly that part situated anterior to the second or third pair of legs, is cast alternately to the right and left when the animal is progressing forwards in a straight line (text-figs. 3 and 4), and the antennæ may be alternately extended forwards (Pl. **15**, figs. 14 and 15). The degree of flexure of the head-end varies, and the footprints may form a straight track in spite of the casting from side to side because the anterior one or two pairs of legs may not always touch the substratum. The head and antennæ may be raised and lowered with an irregular rhythm, often about half as frequently as the paces performed by the legs (see silhouettes on text-fig. 5 ; the line 'ant.' represents the upward and downward movements). The antennæ in the downward phase are usually just clear of the ground (Pl. **15**, figs. 11 and 13), but they may at times touch, as at '*a*' in Pl. **16**, fig. 21, where 6 sensory hairs have left scratches on smoked paper on which the animal was walking.

The Changes in Shape of the Body.

The exact shape of a walking animal varies greatly from time to time. The dimensions of one animal at a particular moment are correlated with the relative duration of the backstroke (see pp. 541 and 551 and text-fig. 6), and the longer extensions of the body are usually associated with the faster speeds (see table II, p. 552). The extension of the body determines in part the form of the tracks (see p. 537).

The body tapers anteriorly and posteriorly, and its most obvious changes are the degrees of longitudinal extension. The same animal is seen in Pl. **15**, figs. 14 and 15 and in Manton 1938 a, pl. XIII, fig. 2 ; its length in fig. 14 is 9 % longer than it is in fig. 15, and in Manton 1938 a, fig. 2 the length is about 11 % shorter than in fig. 15. Two other animals are shown in Pl. **15**, by figs. 10 and 13 and by figs. 11 and 12. The length in fig. 13 is 17 % less than it is in fig. 10, and in fig. 12 it is 10 % greater than in fig. 11. Text-figs. 3 to 5 show the data derived from cinematograph records of a fourth animal. Outlines of the body are given above at successive intervals of 1 second, and below at 'L.B.' is recorded the length of the body in mm, at the end of each second. In text-fig. 5A a length of 58 mm. is constant for almost all of the record, in text-fig. 5B the length decreases from 75–72 mm., in text-fig. 4 the length oscillates between 65 and 68 mm., and in text-fig. 3, where the animal is starting to walk from a stationary position, a stationary length of 51 mm. increases to a walking length of 58 mm. and this again increases to 67 mm.

When the body length increases its thickness decreases (see text-fig. 6, p. 554); more of each leg is visible in dorsal view (compare Manton, 1938 a, pl. XIII, fig. 2 with Pl. **15**, fig. 15), and the heights of the dorsal and ventral surfaces above the ground are changed. An animal which showed a maximum longitudinal extension of 75 mm. carried the dorsal and ventral surfaces of its body 5·2 and 1·3 mm. respectively above the ground at their highest points. The same animal on two occasions showed a walking length of 67 mm., it was performing slightly different speeds and had different shapes. The heights of the dorsal and ventral surfaces above the ground were 5·5 and 1·0 mm. respectively on one occasion and 6·0 and 1·2 mm. on the other ; and the highest point was located about segments 6–7 on the former occasion and segments 8–9 on the latter, when the animal was walking more slowly. Thus an alteration of 8 mm. in body length was associated with an alteration in dorso-ventral thickness of 0·9 mm. at the thickest point. The width of the body also changes, this same animal being about 0·7 mm. wider at a body extension of 58 mm. than at

one of 67 mm. Thus the bases of the legs at the shorter extension of the body must be situated slightly further from the middle line, and slightly nearer to the ground, than at the longer extensions. Changes in the shape of the legs are considered below (p. 533).

In text-fig. 2 *a–c* are shown the distances between the successive leg bases at three extensions of the body of the same animal. The changes in length are fairly uniform throughout the body, including the head end in front of the first pair of legs and the tail end behind the nineteenth pair. It is difficult to measure accurately the distances between successive legs in the absence of clearly defined segmental fixed points. An estimate of these distances can best be made from a series of photographs of the same animal in lateral view. In dorsal view (Pl. **14**) the distances between successive legs may appear to change considerably during each cycle of leg movements when successive legs are in unlike phase (see white dots on frames 2 and 8, Pl. **14**)*, and they appear to remain much the same if successive legs are in almost the same phase (see white dots on frames 3 and 9, Pl. **14**)*. Actually the bases of the legs are obscured by a band of lateral longitudinal muscles bulging above them (see below), and the white dots do not in fact depict the inter-limb distances. These distances do not change in association with the cycle of limb movements, as they do in *Nereis* and arthropods showing lateral undulations of the body. If the inter-limb sections of the lateral longitudinal musculature did change in length, a curvature of the body would result when legs of a pair were in opposite phase, and when successive legs showed a small phase difference. The body remains straight under such conditions, and thus no extensive cyclical changes in the length of the lateral body wall muscles can accompany the limb movements. In *Nereis* Gray (1938) has shown that the motive power is almost entirely derived from the longitudinal muscles of the body, and the adductor muscles of the parapodia probably play a very subordinate rôle in the propulsion of the animal. In Peripatus the reverse is the case, and the major propulsive force must come from the extrinsic limb muscles. It is probable that here the primary function of the longitudinal body musculature is the maintenance of a rigid body wall by interaction with the antagonistic circular, dorso-ventral, and oblique muscles. A firm body wall, such as provided by the stiff integument of most arthropods, will provide fixed points for the operation of extrinsic limb muscles.

A reduction in the propulsive force provided by the longitudinal body muscles and an increase in that supplied by the extrinsic muscles of the limbs must have been an important step in the evolution of limbs for terrestrial locomotion. (See also p. 563). The mechanical basis for the observed relationship between the gait and the proportions of a body segment have not yet been studied. However the recognition of this relationship is of considerable importance, as it provides a functional explanation for the major body forms to be found among the Myriapoda (see Part II), and it also suggests a functional reason for the origin of a haemocoel (see p. 564).

The Movements and Shapes of the Leg.

The limbs of Peripatus extend outwards ventro-laterally raising the lower surface of the body clear of the ground (Pl. **15**, figs. 10–13). Not all the legs touch the substratum; the rudimentary 20th pair in *P. sedgwicki* are not long enough, and Brues (1935) records that the last one or two pairs and the first three pairs in *E. vespucchi* are carried stationary over the substratum. In the specimens of *P. moseleyi* here considered, 22 pairs of legs are locomotory, and in *P. sedgwicki* there are 19 such pairs, but the most anterior and posterior legs do not always touch the ground although they often do so.

The angle at which the legs project from the body in the transverse plane varies individually, and to a small extent in the same animal at different times. The legs are more ventrally directed in the two animals shown in Pl. **15**, figs. 10, 13, 14, and 15 than in the two animals shown in figs. 11 and 12 and in Pl. **14**. The angle varies in

* The dots have been marked on the photographs and were not present on the animal.

association with turning and straightening movements (see p. 557), as seen in Pl. **16**, fig. 16, and with variations in the degree of extension of the legs, see below (see also Manton, 1938, Pl. 1).

The anterior and posterior legs are slightly shorter than those in the middle region, and the first and second pairs are usually more upright than those at the posterior end of the body (Pl. **14**). Thus the tips of the anterior legs are put on the ground closer to the middle line than those of the posterior legs, and the tips of the legs in the middle region are put down farthest from the middle line. Where the body is widest the distances between the tips of the limbs of a pair is greatest. In the animal shown in Pl. **14** and text-fig. 2 *a–c* legs 1 are put down about 2·3 mm. from the middle line, this distance increases to 4·0 mm. at legs 7 and 8 and decreases to 2·5 mm. at legs 19. In animals with more vertically directed legs, as in Pl. **15**, figs. 10 and 14, all the limb-tips are placed relatively nearer to the middle line. In text-fig. 7*a* the dimensions of another animal are shown in which the widest span is by legs 11 and 12 instead of legs 7 and 8, this specimen may have been a female containing fairly bulky embryos.

The extrinsic limb musculature is inserted on to the body wall ventrally and dorso-laterally. The dorsal ' promotors ' and ' remotors ' (Snodgrass' 1938 terminology) pass upwards from the limb mainly internal to the lateral longitudinal muscles, reaching the outer body wall just dorsal to these muscles and well below the level of the pericardial floor *. In some, but not all, specimens the tension on these ' promotors ' and ' remotors ' appears to cause the lateral longitudinal muscle to bulge outwards between their insertions and the base of the limb †. This bulge appears as a pale stripe lying above the limbs in Pl. **15**, figs. 10–13, occupying nearly one third of the visible distance between the bases of the legs and the dorsal outline, and in some specimens it overhangs the bases of the legs. In many species this part of the body is coloured differently from the dorsal surface (see Sedgwick, 1888, Pls. **37** and 39).

The stepping movements of the legs vary in some respects in different individuals. On the forward stroke the leg may be raised to an almost horizontal position in some animals, as in Pl. **15**, figs. 11 and 12, or the foot may be raised only just clear of the ground in others, as in Pl. **15**, figs. 10 and 13. On both forward and backward strokes the leg is held approximately straight from its junction with the body (Pl. **14**); there are no defined joints or movable sections of the limb as in other arthropods. On a hard substratum the tips of the limbs are in contact with the ground for almost the whole of the backstroke, but when walking on paper covered by zinc oxide powder the limbs may touch the ground for the middle half or even less of the backstroke, so that the tips move forward relative to the ground although carrying out part of the backstroke, which then becomes propulsive only in part. Since the leg extends outwards in an approximately straight line during the propulsive backstroke, and since there are no undulations of the body, the length of the leg must change during each backstroke, being longest at the beginning and end, and shortest when the leg extends outwards in the transverse plane. Each leg is put down after the one in front of it is raised, as noted by Moseley (1874) and Bouvier (1905.)

When the animal is stepping evenly, the length of the stride taken by each leg is constant for any given speed of walking, and so is the distance which the base of each leg is carried forwards during the backstroke; this distance and the length of stride become greater with an increase in the speed (see p. 536). The stride lengths range from 2·2 to 4·1 mm. in Pls. **16** and **17**, figs. 18–22 and 25 which show the tracks left by an animal of about 50 mm. length, but greater lengths occur in

* In *Peripatopsis* the bulk of these muscles pass internal to both lateral longitudinal muscles, in *Peripatoides novae-zealandiae* Snodgrass (1938) finds that the dorsal promotor passes external to the internal latero-dorsal longitudinal muscle.

† The cause of this condition is unknown, it may be connected with the amount of connective tissue present, which is often relatively greater in older animals which also tend to show more vertically directed legs.

other gaits. Since the anterior and posterior legs are shorter than those in the middle region, the shorter legs must swing through greater angles in order to achieve the same length of stride. The angle of swing of a leg is difficult to record directly because of uneven stepping which occurs under conditions needed for cinematography (see p. 542) and because of the oblique position of the limbs. The apparent position of the legs in dorsal and in lateral views show average angles of swing up to 92° for legs 2 and 17 and of 63 -83° for leg 8 at a brisk but not maximum speed of walking *.

It is probable that the length of the leg changes at different speeds of walking. Firstly, the distances that the base of the leg is carried forwards during the backstroke range from 2·5–3·5 mm. at speeds of 7–10 mm. per sec. in an animal whose walking length varied from 58–75 mm. It is impossible to measure directly the length of the leg with accuracy in the absence of fixed points. However, a transverse section of the body can be drawn from the dimensions recorded in the films, and the axis of a leg projected from a cylindrical trunk can be measured. If the length of this axis remains constant (apart from changes in length occurring during the backstroke), the leg would have to swing through angles differing by 30° to give distances of 2·5 and 3·5 mm. traversed during the backstroke. If however the length of the axis changes proportionately to that of the body, the axis of the leg would only have to swing through angles differing by about 7° to achieve these distances traversed on the backstroke. It was impracticable to measure the angles of swing appropriately to determine the extent of the changes in the angle of swing. Secondly, the distance between the tips of the limbs of a pair can be measured from a series of photographs in dorsal view, and from recorded footprints. The animal of mean length of 66 mm. showed almost the same distances between legs of a pair at a slow speed and extension of 58 mm. as at a faster speed and extension of 67 mm. The recorded footprints of another animal show the footprints lying nearer to the middle line at lower than at higher speeds. Since the bases of the legs at a minimal extension of the body lie further out and nearer to the ground than they do at greater extensions of the body, the formation of footprints at the same or at greater distances from the middle line at greater extensions of the body must indicate a slight elongation of the leg at the greater extensions. The intrinsic limb musculature is of the same type as that of the body wall, and can presumably carry out comparable alterations in length. It is thus probable that the legs change in length as does the body in relation to the speed of walking, and that at the higher speeds the greater distance travelled by the base of the leg during the propulsive backstroke is achieved partly by an increase in the angle of swing of the leg, and partly by elongation of the leg itself. Changes in longitudinal extension of both body and legs, such as described above, are unusual in the Arthropoda where a rigid integument precludes their occurrence. They might be looked for among certain soft skinned insect larvae provided with legs. Changes in the effective length of the leg during each pace are necessary in most walking Arthropoda, but are done by alterations in the angles of flexure between the several joints.

The Walking Movements.

In *starting to walk* the anterior pair of limbs steps first, and the stepping movement spreads successively to the posterior pair in about 3½ secs., the body at the same time increasing its length by about one-fifth (text-fig. 3). The waves of limb movement pass forwards along the body, as in many arthropods and in polychaetes such as *Nereis*, traversing the body in from 2–6 secs. Peripatus may sometimes resemble *Nereis* in the cycle of limb movement being propagated forwards more slowly than the backwards spread of the starting movements, but the difference between these speeds in Peripatus is not so great as in *Nereis* (see Gray, 1938, text-fig. 1).

* 8 mm. per sec. by an animal of mean length of 66 mm.

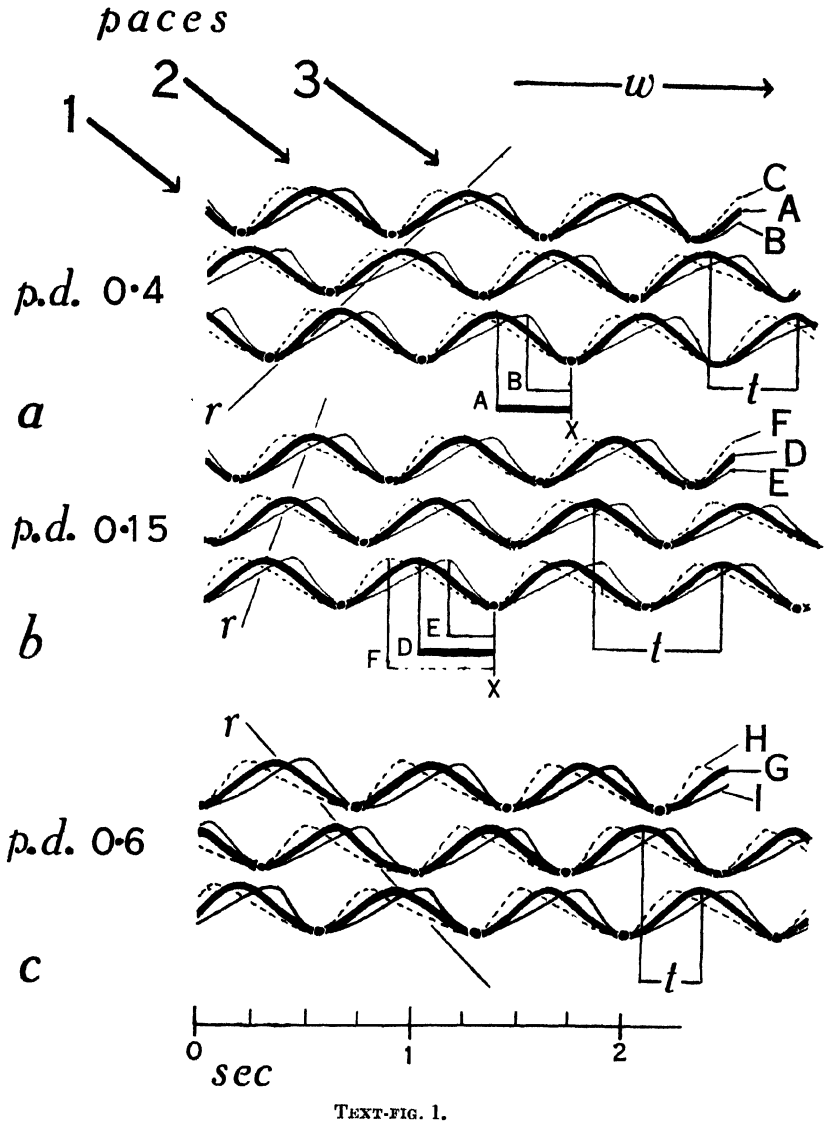
The limb movements vary from time to time, although one type of movement can be maintained for considerable periods. Several *gaits* may be recognized, which result in different speeds of walking and in different patterns of footprints, but intermediate movements exist.

An analysis of the cinematograph records and footprints of Peripatus can best be approached by a consideration of text-fig. 1, which illustrates different gaits. Each gait is characterized by (1) the relative duration of the forward and backward strokes, which will be referred to as the ' pattern ' of the gait, (2) the duration of the whole pace, i.e. one forward and one backward stroke, (3) the angle of swing and the degree of extension of the leg, and (4) the phase difference between successive legs. The numerical data appertaining to text-fig. 1 are arbitrary. The movements of three successive legs of a series are shown, progress being from left to right. A line sloping upwards and to the right represents a forward swing of the leg when it is held clear of the ground, and a line sloping downward and to the right represents a backward stroke when the tip is in contact with the ground. It is assumed that in all gaits the duration of a pace is constant (0·71 sec., which is 10 frames of the cinematograph records), that the legs are of equal lengths and are swung through equal angles, and that a gait of a pattern 'A' results in a speed of 8 mm. per sec. The lines depicting the successive legs are spaced apart for clarity, but since all the legs of one side of the body can use approximately the same footprint, these lines should in reality be spaced closer together. The backstrokes of successive legs which can share the same footprints are marked by the oblique arrows ' paces 1, 2, 3 '. In text-fig. 1*a* the phase difference between successive legs is 0·4 and in text-fig. 1*b* it is 0·15 (i.e. a leg is put down 0·4 or 0·15 of the duration of a pace in advance of the leg in front), these values represent the extremes found in the records. In text-fig. 1*c* a phase difference of 0·6 is shown. No phase differences of over 0·5 are found in Peripatus, but such values are present in some Myriopoda (see Part II). If the same footprint is used by successive legs a phase difference of 0·5 and is mechanically impossible for ' bottom ' or ' middlegear ' gaits as it would cause stumbling (see below).

The pattern of the movement at each phase difference is shown by the lines A–I. The thick lines A, D and G represent legs stepping with forward and backward strokes of equal duration ; such gaits can conveniently be referred to as of pattern (5 : 5 or ' middle gear ' gaits, see p. 553). The thin lines B, E, and I show legs stepping with a long (0·5 sec.) forward swing and a short (0·2 sec.) backward stroke, and such gaits can be referred to as of pattern (7 : 3 or ' top gear ' gaits, see p. 555). The dotted lines C, F, and H represent legs stepping with a short (0·2 sec.) forward swing and a long (0·5 sec.) backward stroke, and such gaits can be referred to as of pattern (3 : 7 or ' bottom gear ' gaits, see p. 553). When all legs of one side of the body use the same footprint, gaits C, G, and H would be mechanically impossible if the angle of swing of the leg remained the same, because a leg cannot be put down on a footprint until the latter is vacated by the leg in front ; however, such gaits might occur if the angle of swing were reduced, but the speed of a C gait at a small angle of swing would be very slow (see also pp. 549, 550 and 555).

The percentage of legs which are in contact with the ground at one moment differs in the various gaits. This is not a function of the phase difference, but is solely determined by the proportion of time spent on the backstrokes. In gait F 70 %, in gaits A and D 50 %, and in gaits B, E and I 30 %, of the legs in a series will be in contact with the ground at once (see also p. 552 and Appendix I).

The slope of the line ' r ' joining comparable positions of the legs in text-fig. 1*a–c* shows the *rate and direction of transmission of the metachronal waves of limb movement* along the body. If this line slopes towards the top of the page the wave will appear to travel forwards (text-fig. 1*a* and *b*), and if it slopes towards the bottom of the page the wave will appear to travel backwards (text-fig. 1*c*), and at the rates



TEXT-FIG. 1.

Different patterns of stepping movements of three successive legs of a series are shown by the undulating lines A–I, progressing in the direction of the arrow '*w*'. The phase difference between successive legs is 0·4 in fig. 1*a*, 0·15 in fig. 1*b*, and 0·6 in fig. 1*c*. The vertical lines X mark the end of the backstroke of all gaits. The horizontal lines 't' show the time interval between one leg and the next behind it being put on the ground. The oblique arrows 'paces 1–3' show the backstrokes of successive legs which can share the same footprints. The line 'r' shows the rate of forward transmission of the metachronal waves of limb movement. In the gaits indicated by heavy lines ½ the legs of a series will be on the ground at once, in those shown by thin lines 3/10ths, and in those shown by dotted lines 7/10ths of the legs will be so situated. For further description see text.

indicated by the slope of line 'r'. The direction and the speed of transmission of the wave is dependent upon the phase difference between successive legs. Phase differences of less than 0·5 give forward transmission, and at increasing speeds as the phase difference decreases; at values of over 0·5 the metachronal waves will pass backwards, and at increasing speeds as the phase difference increases. At a phase difference of 0·5 the wave would appear stationary. In an animal with 19 pairs of locomotory legs moving as in text-fig. 1*a*, the wave of limb movement would traverse the body from tail to head in 6·4 secs., and when moving as in text-fig. 1*b* it would take 1·9 secs. (see also p. 548).

The base of a leg travels forwards continuously. During the backward stroke the tip of the leg is stationary, and the distance travelled by the base of the leg determines the speed of progression of the body. An increase or a decrease in the duration of the forward swing will not influence the speed of progression. The distance travelled by the base of the leg during the backstroke will be the same for different gaits if the angle of swing and length of the leg is the same. Thus if the speed of the animal with a gait of pattern A is 8 mm. per sec. a distance of 2·8 mm. will be traversed during the 0·35 sec. period between the vertical lines X and A (text-fig. 1 *a*) and X and D (text-fig. 1*b*), and also during the 0·2 sec. period between the lines X and B and X and E, and during the 0·5 sec. period between the lines X and F. The speeds of gaits B, D, E and F can then be calculated, and are greatest for (7 : 3) gaits B and E (thin lines, 13·3 mm. per sec.), and least for (3 : 7) gait F (dotted lines, 5·6 mm. per sec.). The phase difference between successive legs can change without influencing the speed.

The length of a stride of a leg is given by the duration of the pace × the speed of progression. The stride in gait F will be 3·9 mm., in gaits A and D 5·7 mm., and in gaits B and E 9·6 mm. Longest strides thus accompany greatest speeds (see also p. 542). Stride lengths are uninfluenced by the phase difference between successive legs.

If the *angle of swing* or the *length of the legs* or both are increased while the pace duration remains the same, the body will be propelled forwards faster. If a distance of 3·2 mm. instead of 2·8 mm. is traversed by the base of the leg during the backstroke, a speed of 9 mm. per sec. will be achieved by gaits A and D, 15·2 mm. per sec. by gaits B and E, and 6·4 mm. per sec. by gait F. If the angle of swing or the length of the legs or both are decreased, the pace duration remaining the same, slower speeds will result; thus if 2·5 mm. is traversed by the base of the leg during the backstroke, gaits A and D will give speeds of 7 mm. per sec., gaits B and E speeds of 11·8 mm. per sec. and gait F a speed of 5·0 mm. per sec. The lengths of the strides are correspondingly increased or decreased (see also p. 542).

The pattern of the footprints is determined by the duration of the pace, the speed of progression, the pattern of the gait and phase difference between successive legs, and by the degree of extension of the body and limbs. Each foot may be put down approximately upon the same place as used by the leg in front, and then a rounded common mark is formed by all the legs of one side of the body at each pace ('pace 1' etc., on text-fig. 1), and a series of such marks will lie on either side of the middle line, and be separated by the length of the stride (Pl. 16, figs. 20 and 21). Alternatively each foot may be put down either in front or behind the footprint left by the leg in front, and then the footprints of all the legs of the body will form elongated sets, such as seen in Pl. 16, figs. 18 and 19. If each set is longer than the length of the stride, the successive sets will overlap as in fig. 18.

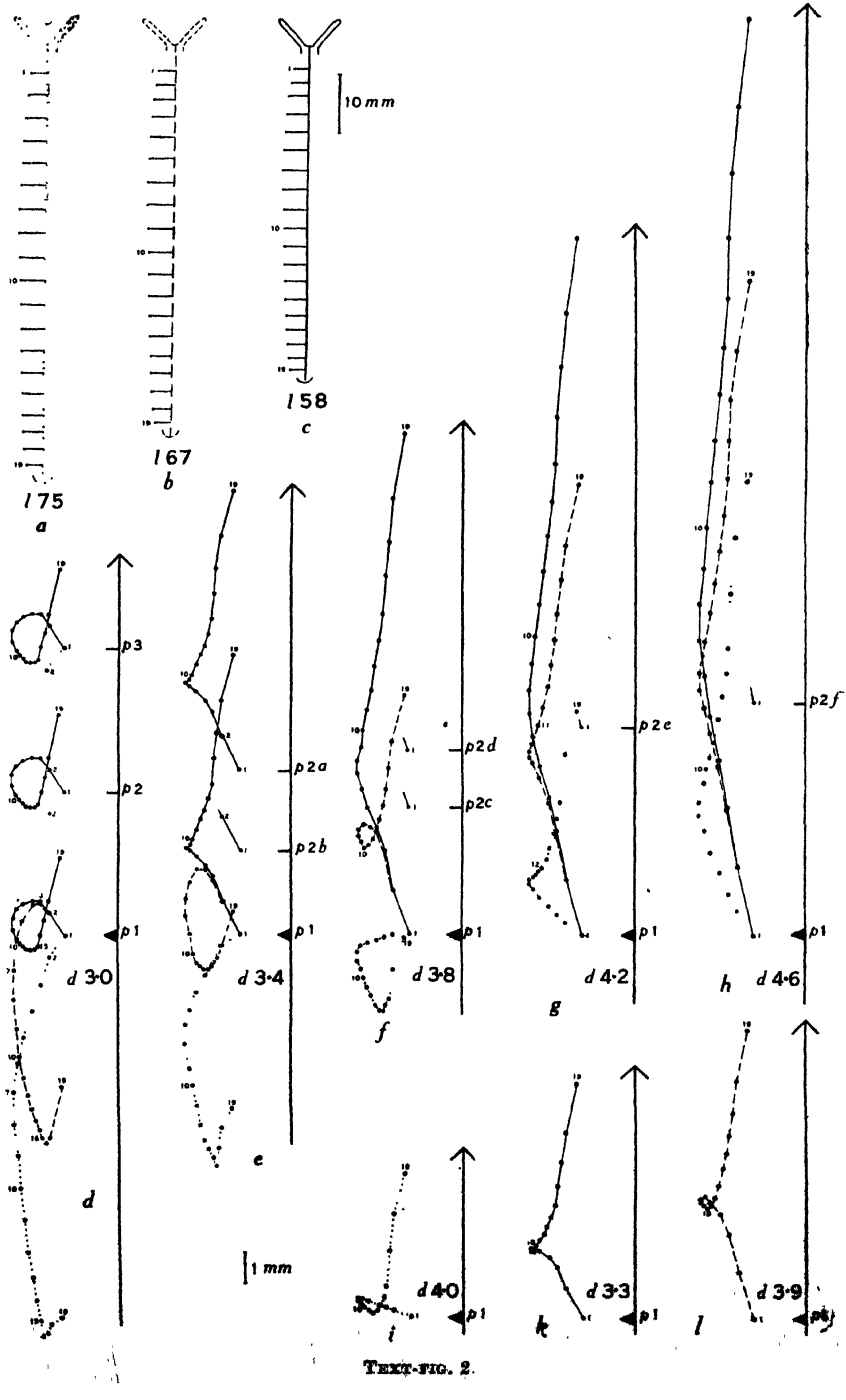
The time interval between the beginning of the backstrokes of two successive is legs shown by the line 't' in text-fig. 1. It is of the same duration for all gaits with the same phase difference and duration of pace; thus 't' is 0·42 sec. for gaits A

and B, 0·62 sec. for gaits D, E and F, and 0·28 sec. for gait I. The distance 'd' travelled during time 't' will be different for each gait, thus for gaits A, B, D, E, F and I it is 3·4, 5·6, 4·9, 8·5, 3·5 and 3·7 mm. respectively. The position of the n+1th footprint relative, to that formed by the nth leg in front of it is given by the distance 'd' minus the distance 's' between the middle of the bases of the two successive legs. (The distance 's' varies individually and in different parts of the body, and is altered by changes in longitudinal extension of the body, see above.) When the resultant of (d–s) is positive the n+1th, footprint will lie at that distance anterior to nth footprint, and when it is negative footprint n+1 will lie behind footprint n, and when it is zero footprint n+1 will lie at the same antero-posterior level as footprint n. The theoretical position of each footprint of a given gait can now be plotted. The antero-posterior co-ordinate is given by (d–s) and the transverse co-ordinate by the distance from the middle line of the penultimate pad of setae near the tip of each leg, this distance varies with the segment and with the degree of extension of of the animal.

A variety of gaits and speeds exist between certain extremes for any one animal. Speeds of 5–10 mm. per sec. are shown by a full sized *P. sedgwicki* of mean length of of 66 mm. The resultants of 'd' over this range lie between 3 and 7·3 mm. The theoretical patterns of the sets of footprints formed by this animal when 'd' is 3·0, 3·4, 3·8, 4·2 and 4·6 mm. are shown in text-fig. 2. The vertical arrows represent the sagittal line of the body and of the track, and show the direction of walking, and left footprints only are drawn. The middle of each footprint is indicated by a dot, and a line joins the footprints of successive legs which form each set. Footprints of legs 1, 10 and 19 are marked, and the numbers of the intervening footprints are usually omitted. The positions of the footprints of the first pace by leg 1 are plotted on the same horizontal level for the different values of 'd', and are marked 'p.1.' Three different sets of footprints are shown for pace 1 at each value of 'd'. That marked by a continuous line is formed by the animal walking at a minimal extension (58 mm.) with dimensions as shown in text-fig. 2*c*; that marked by a broken line line is formed by the animal at a moderate length (67 mm.) as in text-fig. 2*b*: and that marked by a dotted line is formed by the same animal at a maximal length (75 mm.) as in text-fig. 2 *a*. As the value of 'd' increases there is a tendency for each set to spread further forwards from the footprints of the first leg.

The sets of footprints formed by the second and third paces of all legs are drawn for the body length of 58 mm. in text-fig. 2*d*, 'p.2.' and 'p 3.' marking the antero-posterior levels of the footprints of leg one. The beginnings of the sets corresponding with the longer body length (dotted line) are shown only as far as the footprints of leg two, the sets corresponding with the moderate body length (interrupted line) lie superimposed on those shown for a length of 58 mm. as far as the footprints of leg two, and are not indicated. In text-fig. 2*e* the set of footprints formed by the second pace for a body length of 58 mm. is shown in full (continuous line) starting at the level 'p.2.a'. It is found that more than one gait possess the same value for 'd' and that the lengths of the strides of such gaits may or may not be the same (see p. 542). If the degree of extension of the body is the same, the tracks made by gaits with a similar value 'd', but different lengths of stride, will consist of identical sets of footprints separated by distances equal to the various lengths of stride. Thus in text-fig. 2*e* the set of footprints formed by the second pace of gaits with a stride length of 5·6 mm. starts at the level 'p.2.a', while that of gaits with a stride length of 3·9 mm. starts at the level 'p.2.b.', only two footprints being indicated. Similarly in text-fig. 2*f* 'p.2.c.' and 'p.2.d.' represent the levels at which the second set of footprints are formed by gaits possessing a 'd' of 3·8 mm. but different stride lengths.

Each set of footprints may form an almost closed ring, it may be α-shaped, and the end formed by the posterior legs may extend forwards or backwards. When 'd' is 4·2 mm. the sets of footprints formed at all body lengths extend forwards without any loop, and when 'd' is greater than this the sets of footprints extend further


10 mm
158
c
167
b
175
a
p3
p2
p1
d 3·0
d
p2a
p2b
d 3·4
e
1 mm
p2d
p2c
d 3·8
f
p2e
d 4·2
g
p2f
h
d 4·6
d 4·0
i
d 3·3
k
d 3·9
l

TEXT-FIG. 2.

forward, as in text-fig. 2*h*, or to an even greater extent. When compact, circular, or, α-shaped, sets of footprints are formed they are well separated from each other, but the elongated sets overlap). At slow speeds (low values of 'd'), (or if the body were extended) they overlap backwards (dotted lines text-fig. 2*d* and *e*), and at higher speeds (or if the body were more contracted) they overlap forwards (continuous line text-fig. 2*f*–*h*). At a 'd' of 6·4 mm. which is shown by a gait 'E.$\theta_{2\cdot8}$' (see below and table I), each set will be about three times as long as that shown by the dotted line on text-fig. 2*h*, and the overlap will be such that six sets will lie superimposed upon each other so that they can no longer be differentiated in the track.

Sets of footprints formed at different body lengths may possess the same general form at different values of 'd', as shown for example by the continuous line in text-fig. 2*e*, the interrupted line in fig. 2*g*, and the dotted line in fig. 2*h*, but the sets are never replicas of each other. In text-fig. 2*i*, *k*, and *l* shown the sets formed at the three extensions of the body which have the smallest loop in the line joining the footprints, to the nearest 0·1 mm. for 'd' (i.e. if the 'd' value is increased by 0·1 mm. the loop in each case opens out). These three sets are of different sizes, that formed at a 67 mm. extension is longer than those formed at extensions of 58 and 75 mm; this order of overall length is not the same as it is for the sets at the three body extensions in fig. 2*g* and *h*, where the 58 mm. extension of the body gives the longest set. The proportions of the three sets in fig. 2*i*, *k*, and *l* are also unlike, the footprints of leg 10 forms the middle of the loop in fig. 2*i*, it lies beyond the loop in fig. 2*k*, and in fig. 2*l* it lies on the last quarter of the loop. For every change in body extension,

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Legend to Text-fig. 2

Figs. *a*–*c* show walking extensions of the body of 75, 67 and 58 mm. respectively, in the same specimen of *P. sedgwicki* seen in Pl. **14**, and the distances of the tips of the limbs from the middle line. The tips of the limbs are shown at the same distances from the middle line at all three extensions, although these distances are actually slightly less at the shorter extensions of the body.

Figs. *d*–*h* show the calculated left sets of footprints of the animal seen in Pl. **14** and text-fig. 2*a*–*c*, which will be formed at the three extensions of the body (continuous, interrupted and dotted lines) when the distance 'd' travelled in time 't' (see text-fig. 1) is 3·0, 3·4, 3·8, 4·2 and 4·6 mm. respectively. All the main shapes of the sets, are illustrated, as values of 'd' much below 3·0 mm. do not occur during normal walking, and the higher values exhibit the same type of pattern as in fig. *h* but of a more elongated form. For further description of the figures see p. 357. The details of the gaits which will form these footprints are given in table I on the horizontal lines opposite the values of 'd'. Gaits with similar relative durations of forward and backward stroke bear the same letter (A, or B etc) and will be performed at the same extension of the body.

Fig. *d*. 'd' is 3·0 mm., the sets of footprints are repeated at 5·0 mm. intervals, 'p.2' and 'p.3' showing the position of the second and third paces of leg 1. The three gaits entered on table I with a 'd' of 3·0 mm. have the same stride lengths and body extensions, so that their tracks will be as shown by the interrupted lines, repeated at intervals of 'p.1'–'p.2' etc.

Fig. *e*. 'd' is 3·4 mm. The six gaits entered on table I for a 'd' of 3·4 mm. have two stride lengths and two body extensions, so that the tracks formed by the three A.$\theta_{2\cdot8}$ gaits will be as shown by the interrupted lines repeated at 'p.2.a', and those formed by the three F.$\theta_{2\cdot5}$ gaits will be shown as by the continuous lines repeated at 'p.2.b'.

Fig. *f*. 'd' is 3·8 mm. The six gaits entered on table I for a 'd' of 3·8 mm. have two stride lengths and two body extensions, so that the tracks formed by the three gaits A.$\theta_{3\cdot2}$ will be as shown by the interrupted line repeated at 'p.2.d', and those formed by the three F.$\theta_{2\cdot8}$ gaits will be as shown by the continuous line repeated at 'p.2.c'.

Fig. *g*. 'd' is 4·2 mm. The two gaits entered on table I for a 'd' of 4·2 mm. have almost the same stride lengths but would probably have different extensions of the body (the B gait has not been recorded from the living animal). The tracks of the B.$\theta_{2\cdot5}$ and A.$\theta_{3\cdot5}$ gaits will be as shown by the dotted and interrupted lines respectively, repeated at 'p.2.e'.

Fig. *h*. 'd' is 4·6 mm. One gait entered on table I for a 'd' of 4·6 will probably form tracks as shown by the dotted line and repeated at '2.p.f' (a B gait has not been recorded from the living animal, but would probably show a body extension as for the E gaits).

Figs. *i*–*l* show the sets of footprints formed at the three body extensions which possess the smallest loop in the line joining the successive footprints, taken to the nearest 0·1 mm. for 'd'. For further description see text.

or in the value of ' d ', a set of footprints is formed which is unlike any other. The sets of footprints covering the smallest area are formed by the three body extensions when the ' d' value is 3·0, 3·4 and 3·8 mm. respectively (see the continuous, interrupted and dotted lines on text-fig. 2*d*, *e* and *f*); a particularly compact appearance may result from the failure of legs 1 and 19 to touch the ground, so that the α-like form is reduced to a dot, see text-fig. 2*d* continuous line.

The sets of footprints shown by the continuous line in text-fig. 2*e* and by the broken and dotted lines in text-fig. 2*g* show a distinct kink between footprints 6 and 9. This point corresponds with the loop shown by the continuous line in text-fig. 2*d* and the broken line in text-fig. 2*e* and *f*. The position of this kink or bend is determined by the widest part of the animal, and by the relative lengths of the anterior and posterior segments. In this particular specimen (Pl. **14** and text-fig. 2*a–c*) limbs 7 and 8 are put down furthest from the middle line, and leg 10 lies almost mid-way between leg 1 and the posterior end of the body. In the tracks formed by the animal shown in text-fig. 7*a* at a ' d ' of 3·5 mm (text-fig. 7*b*), the bend in each set occurs at footprints 10–11 and lies nearer to the opposite end of the set (compare with text-fig. 2*e*, continuous line). The animal shown in text-fig. 7*a* has its widest point near legs 10 and 11, and the body length behind leg 10 is relatively greater than it is in the animal shown in text-fig. 2*a–c*. Thus very small differences in bodily shape cause conspicuous differences in the tracks. Factors which effect the form of the tracks are further considered on pp. 542 and 550.

In table I details of various *gaits which might be performed* by this same specimen of *P. sedgwicki* (Pl. **14** and text-fig. 2*a–c*) are arranged under progressive values for ' d '. They are calculated as shown above, taking values for the duration of the pace, the duration of the backstroke, and the phase difference between successive legs which are shown by the cinematograph records of this animal (see text-figs. 3–5 and below). Pace durations of 10 frames (0·71 sec.) as in text-fig. 1, of 11 frames (0·785 sec.) and of 12 frames (0·86 sec.) are shown in the vertical columns I–III. and the general characters of the gaits at these three pace durations are entered above. The patterns of gaits A–E are seen in text-fig. 1.• The duration of the backstroke in gaits A and D is equal to that of the forward stroke, in gaits B and E the backstroke is faster and in gait F it is slower than the forward stroke. The durations chosen for the backstrokes are 3·5, 4·0 and 4·5 frames (0·25, 0·28 and 0·32 sec.) in gaits B and E, they are 5·0, 5·5 and 6·0 frames (0·35, 0·39 and 0·43 sec.) in gaits A and D, and 6·5, 7·0 and 7·5 frames (0·46, 0·50 and 0·53 sec.) in gait F. (A backstroke of 3 frames (0·21 sec.) as shown in text-fig. 1 for gaits B and E is actually too short to be performed by the animal.) In gaits A and D the phase difference between successive legs is 0·4 and in gaits D, E and F it is 0·15, as in text-fig. 1.

TABLE I

The calculated gaits of a specimen of *P. sedgwicki* shown in text-fig. 2*a–c* and Pl. **14**, arranged under increasing values for ' d ' (the distance travelled in time ' t ', the interval between one leg and the next behind it being put on the ground (see text-fig. 1) The general patterns of gaits A–F are shown in text-fig. 1. The durations of the forward and backward strokes of gaits A and D are as 5 : 5 in all columns ; those of gaits B and E are as 6·5 : 3·5, 6·4 : 3·6 and 6·3 : 3·7 in columns I–III respectively , and those of gaits F are as 3·5 : 6·5, 3·6 : 6·4 and 3·7 : 6·3 in columns I–III respectively. The phase difference between successive legs in gaits A and B is 0·4 and in gaits D, E and F is 0·15, as in text-fig. 1*a* and *b*. The numbers entered after θ indicate that the angles of swing and the extension of the legs are such that distances of 2·5, 2·8, 3·2, and 3·5 mm. respectively are traversed by the base of the leg during the backstroke (only one entry for $\theta_{2\cdot5}$ is given). Speeds are given in mm. per sec., and lengths of stride in mm. ; both are expressed to the nearest 0·1 mm., certain small differences between the gaits are thereby masked. The entries in italics and in brackets are too fast for the animal to perform, and those in italics alone are of doubtful practicability. The particulars of the gaits are calculated from the data given at the top of each column, and from the assumption that gait A, $\theta_{2\cdot5}$ in column I gives a speed of 8 mm. per sec.

TABLE I.

Distance 'd' travelled in time 't'	I			II			III		
	Duration of pace 10 frames (0·71 sec.)			Duration of pace 11 frames (0·785 sec.)			Diuraton of pace 12 frames (0·86 sec.)		
	Duration of forward stroke	Duration of back stroke	Gaits	Duration of forward stroke	Duration of back stroke	Gaits	Duration of forward stroke	Duration of back stroke	Gaits
	5 frames (0·35 sec.)	5 frames (0·35 sec.)	A, D (5 : 5)	5·5 frames (0·39 sec.)	5·5 frames (0·39 sec.)	A, D (5 : 5)	6 frames (0·43 sec.)	6 frames (0·43 sec.)	A, D (5 : 5)
	6·5 frames (0·46 sec.)	3·5 frames (0·25 sec.)	B, E (6·5 : 3·5)	7 frames (0·50 sec.)	4 frames (0·28 sec.)	B, E (6·4 : 3·6)	7·5 frames (0·53 sec.)	4·5 frames (0·32 sec.)	B, E (6·3 : 3·7)
	3·5 frames (0·25 sec.)	6·5 frames (0·46 sec.)	F (3·5 : 6·5)	4 frames (0·28 sec.)	7 frames (0·50 sec.)	F (3·6 : 6·4)	4·5 frames (0·32 sec.)	7·5 frames (0·53 sec.)	F (3·7 : 6·3)
	Gait	Speed	Stride	Gait	Speed	Stride	Gait	Speed	Stride
mm.									
3·0	A, $\theta_{2\cdot5}$	7·0	5·0	A, $\theta_{2\cdot5}$	6·4	5·0	A, $\theta_{2\cdot5}$	5·9	5·0
3·4	A, $\theta_{2\cdot8}$	8·0	5·7	A, $\theta_{2\cdot8}$	7·1	5·7	A, $\theta_{2\cdot8}$	6·7	5·7
	F, $\theta_{2\cdot5}$	5·4	3·9	F, $\theta_{2\cdot5}$	5·0	3·9	F, $\theta_{2\cdot5}$	4·6	3·9
3·8	A, $\theta_{3\cdot2}$	9·0	6·4	A, $\theta_{3\cdot2}$	8·2	6·4	A, $\theta_{3\cdot2}$	7·6	6·4
	F, $\theta_{2\cdot8}$	6·1	4·4	F, $\theta_{2\cdot8}$	5·6	4·4	F, $\theta_{2\cdot8}$	5·2	4·5
4·0	—	—	—	—	—	—	$B, \theta_{2\cdot5}$	7·8	6·7
4·1	—	—	—	B, $\theta_{2\cdot5}$	8·9	7·0	—	—	—
4·2	B, $\theta_{2\cdot5}$	10·0	7·1	—	—	—	—	—	—
	A, $\theta_{3\cdot5}$	10·0	7·0	—	—	—	—	—	—
4·3	D, $\theta_{2\cdot5}$	7·0	5·0	D, $\theta_{2\cdot5}$	6·4	5·0	D, $\theta_{2\cdot5}$	5·9	5·0
	F, $\theta_{3\cdot2}$	7·0	5·0	F, $\theta_{3\cdot2}$	6·4	5·0	F, $\theta_{3\cdot2}$	5·9	5·1
4·4	—	—	—	—	—	—	$B, \theta_{2\cdot8}$	8·7	7·4
4·6	—	—	—	B, $\theta_{2\cdot8}$	10·0	7·8	—	—	—
4·7	($B, \theta_{2\cdot8}$	*11·5*	*8·0*)	—	—	—	—	—	—
4·9	D, $\theta_{2\cdot8}$	8·0	5·6	D, $\theta_{2\cdot8}$	7·2	5·6	D, $\theta_{2\cdot8}$	6·7	5·6
5·1	—	—	—	—	—	—	$B\theta_{3\cdot2}$	10·0	8·6
5·2	—	—	—	($B, \theta_{3\cdot2}$	*11·8*	*8·8*)	—	—	—
5·3	($B, \theta_{3\cdot2}$	*12·8*	*9·0*)	—	—	—	—	—	—
5·5	D, $\theta_{3\cdot2}$	9·0	6·4	D, $\theta_{3\cdot2}$	8·2	6·4	D, $\theta_{3\cdot2}$	7·6	6·4
5·7	—	—	—	—	—	—	E, $\theta_{2\cdot5}$	7·8	6·7
5·8	—	—	—	E, $\theta_{2\cdot5}$	8·7	7·0	—	—	—
6·2	*E*, $\theta_{2\cdot5}$	*10·0*	*7·1*	—	—	—	—	—	—
6·4	—	—	—	—	—	—	E, $\theta_{3\cdot8}$	8·7	7·4
6·5	—	—	—	*E*, $\theta_{3\cdot8}$	*9·5*	*7·8*	—	—	—
7·0	(*E*, $\theta_{2\cdot8}$	*11·2*	*8·0*)	—	—	—	—	—	—
7·3	—	—	—	—	—	—	*E*, $\theta_{3\cdot2}$	*10·0*	*8·6*
7·5	—	—	—	(*E*, $\theta_{3\cdot2}$	*11·2*	*8·8*)	—	—	—
8·0	(*E*, $\theta_{3\cdot2}$	*12·8*	*9·0*)	—	—	—	—	—	—

[*For legend to Table I, see p.* 540.

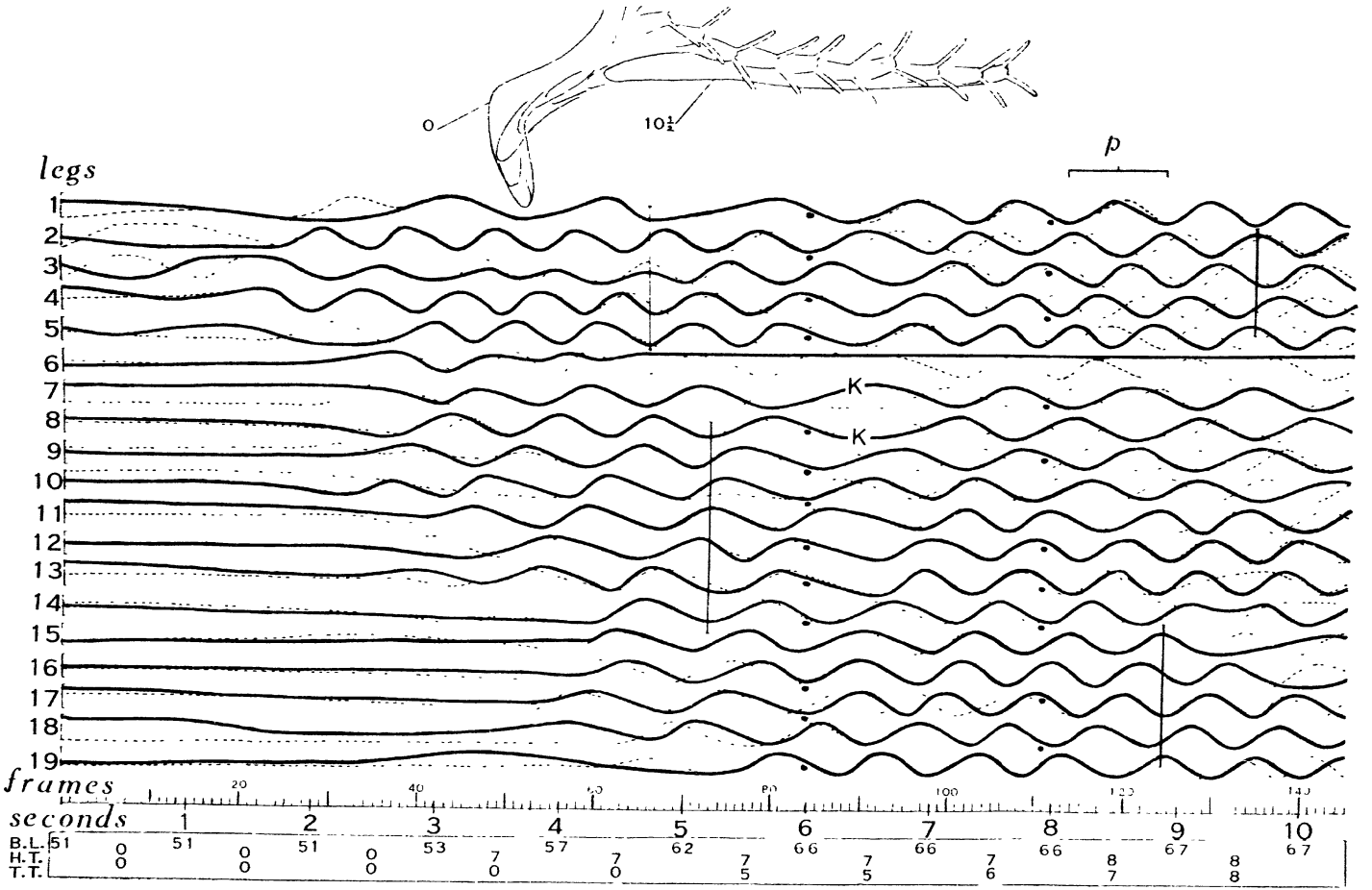
Alternative values are given for a factor 'θ' which represents the angle of swing of the legs. The shorter anterior and posterior legs execute greater angles of swing than the longer middle legs, so that the same distance is travelled by the bases of all the legs during their backstrokes (p. 533). Greater speeds may be achieved by an increase in both the extension of the legs and their angles of swing (p. 533). When the angles of swing and the extensions of the legs are such that the bases travel 2·5 mm. during the backstroke, '$\theta_{2\cdot5}$' is given beside the letter denoting the pattern of the gait. Similarly when the angles of swing and the extensions of the legs are increased, so that 2·8, 3·2 or 3·5 mm. are traversed by the bases of the legs during the backstrokes, '$\theta_{2\cdot8}$', '$\theta_{3\cdot2}$' and '$\theta_{3\cdot5}$' respectively are given (there is only one entry for $\theta_{3\cdot5}$). These values of θ result in speeds of 7, 8, 9 and 10 mm. per sec. by gait A in column I. At each of the three pace durations (columns I–III) all gaits bearing the same values for θ traverse the same distance during the backstroke. The pattern of the gait and the angle of swing of the leg, the resultant speed in mm. per sec., and the length of the stride performed by the legs are entered on the same horizontal line as their values for 'd'.

Of the 45 different gaits entered in table I, up to 6 possess the same value for 'd'. If the body extension remained constant the sets of footprints formed at different speeds by all gaits with a similar 'd' value would be identical. Actually the body extension for gaits of the A and D patterns may be the same, but that for the F pattern will be shorter and for the E pattern longer. When 'd' is 4·3 mm. almost the same stride length is also shown by the 6 gaits, so that here the distance between successive sets of footprints will be common to all, but gaits of the D and F patterns would be performed at different body extensions, so that two types of track will be formed by the 6 gaits. Where 'd' is 3·4 mm. there are again 6 gaits, but those marked A, $\theta_{2\cdot8}$ have stride lengths of 5·7 mm., and those marked F, $\theta_{2\cdot5}$ have stride lengths of 3·9 mm.; the body extensions of gaits A and F will be different, so that two types of track will be formed with distances of 5·6 and 3·9 mm. between successive sets of footprints of two different forms. It will be noted that two different gaits can give the same speed and stride length, as shown by D, $\theta_{2\cdot5}$ and F, $\theta_{3\cdot2}$ at each of the three pace durations (columns I–III). It will also be seen by reference to either columns I, II or III that a change of phase difference alone will considerably alter the value of 'd' (compare A, $\theta_{2\cdot5}$ and D, $\theta_{2\cdot5}$ or B, $\theta_{2\cdot8}$ and E, $\theta_{2\cdot8}$), and thus will greatly change the pattern of the footprints (see pp. 550 and 556).

Table I shows that the length of the stride tends to increase with increasing speed, but that the length also depends on the duration of the pace. Strides of 3·9 mm. are found at speeds of 4·6–5·4 mm. per sec., strides of 4·4 mm. occur at speeds of 5·2–6·1 mm per sec., and strides of 5·0 mm. at speeds of 5·9–7·0 mm. per sec. etc. Further points emerging from this table are considered on p. 550, and in Part II.

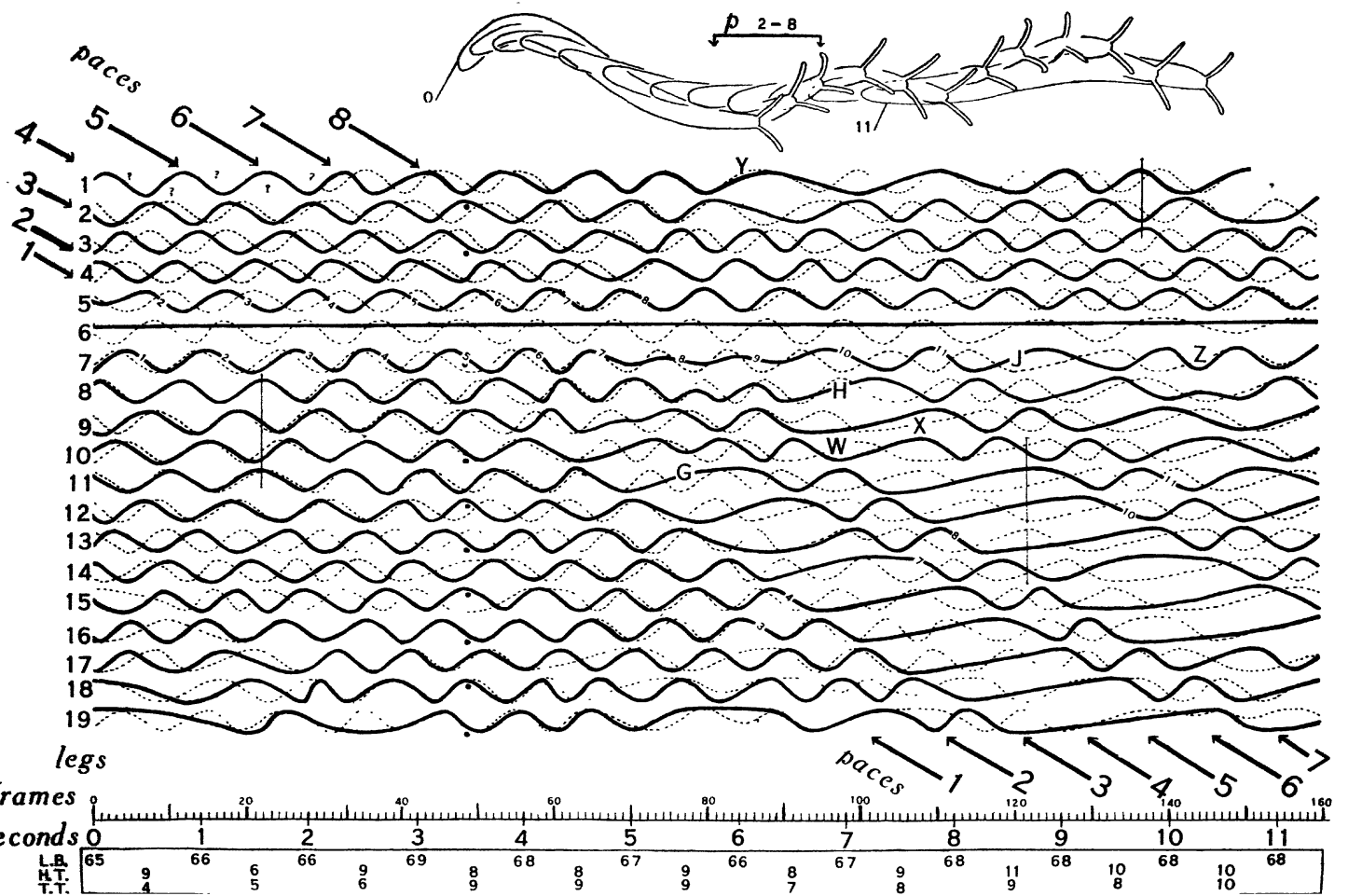
The Cinematograph records of Walking.

The animals normally shun bright light, and all the cinematograph records show a lack of uniformity in the limb movements (see also pp. 548 and 551), due, it is believed, to the stimulatory effect of the illumination. The footprints which were recorded on smoked paper in a dimmer light show that the animal can maintain exactly the same pattern of gait, angle of swing of the leg, pace duration, and speed for considerable periods. It is probable that this uniformity is usual under natural conditions. During uneven stepping compensatory variations occur in the movements of the legs and body, so that the speed of walking is not necessarily altered (see p. 560). In spite of the irregularities occurring under the bright light, the various types of movement of which the animal is capable can be seen in the cinematograph records. Some of the analyses of these records are shown in text-figs. 3–5; in text-fig. 3 the animal is starting to walk from a stationary position; in text-figs. 4 and 5A a walking animal is recorded in dorsal view; and text-fig. 5B is taken from a walking animal in lateral view. The left half of text-fig. 4 shows the most regular section of the films.



TEXT-FIG. 3.

[*For legend see p. 546.*


paces
p 2-8
0
11
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5
6
7
8
3
2
1
Y
J
Z
H
X
W
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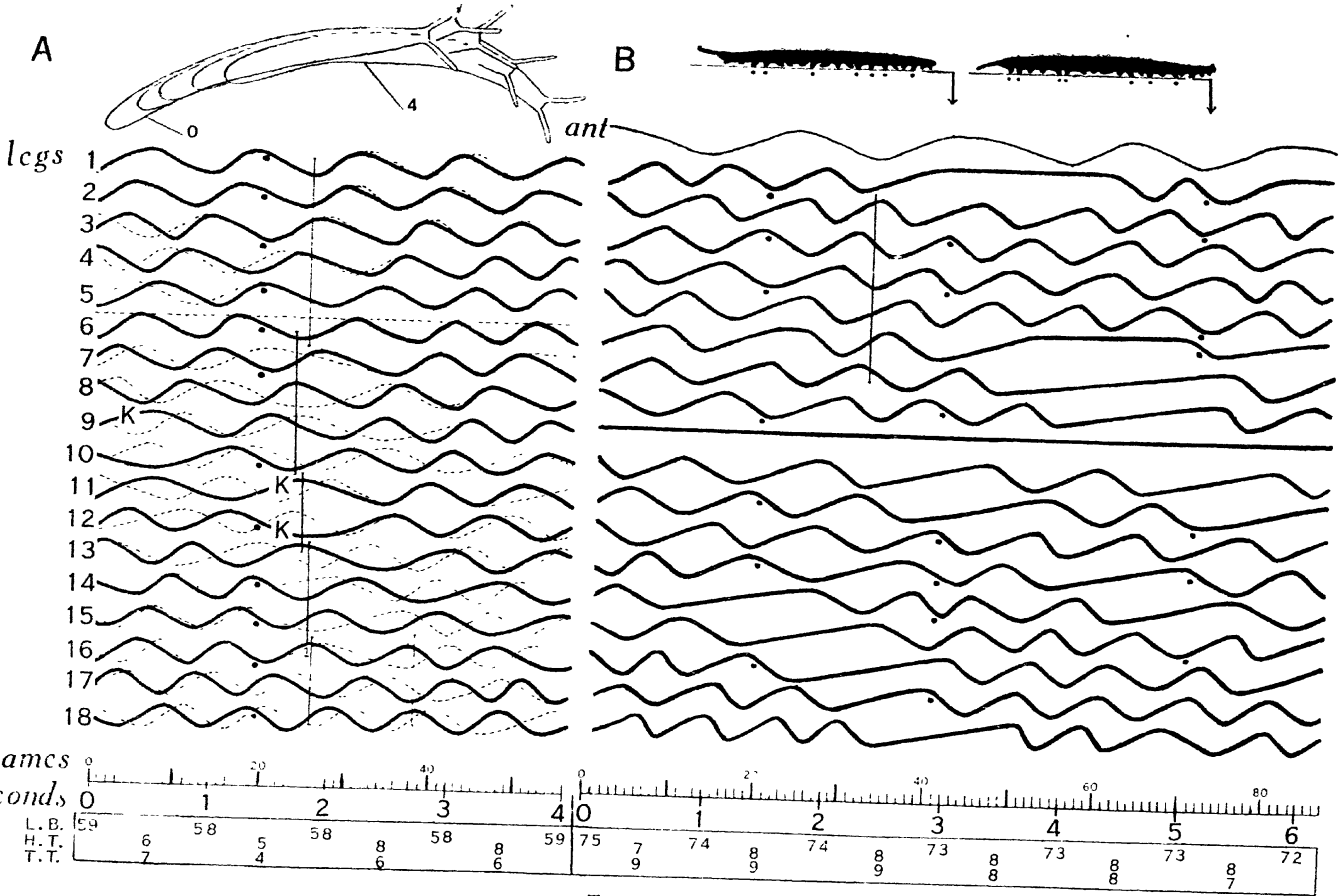
legs
paces 1 2 3 4 5 6 7
frames 0 20 40 60 80 100 120 140 160
seconds 0 1 2 3 4 5 6 7 8 9 10 11
L.B. 65 66 66 69 68 67 66 67 68 68 68 68
H.T. 9 6 9 8 8 9 9 8 11 10 10
T.T. 4 5 6 9 9 9 7 8 9 8 10



TEXT-FIG. 5.

[For legend see p. 546.

TEXT-FIGS. 3–5.

These figures give analyses of four cinematograph films of the same individual of *P. sedgwicki*, showing various gaits, speeds, and extensions of the body. The general form of the records is the same as described for text-fig. 1, p. 534, see also p. 542. The vertical rows of spots mark legs, of the side shown by heavy lines, which are in contact with the ground at one moment.

Text-fig. 3 shows the animal starting to walk from a stationary position at 0 sec. The heavy lines represent the positions of the right legs and the dotted lines those of the left legs. Above are given outlines of the body at the start 'O', at 10 intervals of 1 sec. and at 10½ secs. after the start. The bracket 'p' shows the location of the 12 successive photographs on Pl. **14**. On the right-hand third of the figure, where stepping is well established, the average duration of a pace by the anterior 5 and many other legs is 10 frames (0·71 sec.); the forward and backward strokes are of equal duration, an average of 9–10 legs are in contact with the ground at once, see spots at frame 117. On the middle part of the figure, where all legs have started stepping, the duration of a pace is often up to 13–15 frames (1 sec.); the backward stroke is up to twice the duration of the forward stroke; and up to 14 legs may be in contact with the ground at once, see 13 spots at frame 84. The phase difference between successive legs is small at first, 0·25 and 0·16 between right legs marked by the vertical lines at frames 66 and 73 respectively, and it increases to 0·33 and 0·25 between the vertical lines at frames 134 and 124, and to 0·45 for the anterior legs at the right-hand side of the record.

TEXT-FIG. 4.

The same animal walking at a moderate pace. The left half of the figure shows fairly regular stepping, and the right half shows various irregularities described on p. 549. The footprints were recorded at the same time, see fig. 17, Pl. **16** and text-fig. 8. The heavy lines represent the positions of the right legs and the dotted lines those of the left legs. The oblique arrows 1–8 are approximately in line with the backstrokes of the right legs forming the sets of footprints shown in fig. 17 and text-fig. 8: the backstrokes of the corresponding left legs lie either on the same lines or a little to the right (in advance) and have not been shown by separate arrows. The small oblique numbers on the heavy lines denote the backstrokes of the right legs. The vertical letters G, H and J represent irregularities started by right legs and repeated by those following on the right side; and the letters W, X, Y and Z represent irregularities started by left legs which are propagated backwards; G and W are also seen in text-fig. 8. The initial irregularities of the posterior few legs is associated with a straightening of the posterior end of the body. Above are given outlines of the body at one sec intervals from 0 to 11 secs., 'p.2–8' shows the level of the sets of footprints 2–8 shown in fig. 17 and text fig. 8. On the left half of the figure: the average duration of a pace by most legs is 10 frames (0·7 sec.) with forward and backward strokes of equal duration, and an average of 9–10 legs are in contact with the ground at once, see spots at frame 49; the phase difference between successive legs is 0·3–0·45, see the vertical line at frame 22; the average time interval between one leg being raised from the ground and the next being put in its pace is 1¼ frames (0·12 sec.); and the lengths of stride at paces 6–8 are 5·5–6 mm.

TEXT-FIG. 5A.

The same animal walking more slowly and showing a small phase difference between successive legs and a shorter extension of the body. The heavy lines represent the positions of the left legs and the dotted lines those of the right legs, the nineteenth pair is omitted as it could not be seen clearly in the film. Above are given outlines of body at 1 sec. intervals from 0 to 4 secs. The average duration of a pace by the more anterior legs (which are stepping evenly) is 11 frames (0·74 sec.). The average duration of the forward swing is 4·2 frames (0·30 sec.) while that of the backward stroke is 6·8 frames (0·48 sec.), an average of 12 legs is in contact with the ground at once, see spots at frame 20. The vertical lines at frame 25 show phase differences of 0·2 between legs 1–6, 0·25 between legs 6–10, almost 0·5 between legs 11–13, 0·33 between legs 13–16 and 0·35 between legs 16–18. The average time interval between one leg being raised from the ground and the next being put in its place is 1¾ frames (0·12 sec.). The average pace length by the more anterior legs is 5 mm.

TEXT-FIG. 5B.

The same animal walking more quickly and showing a small phase difference between successive legs and a longer extension of the body. The film was taken in lateral view so that the left legs only are shown. The nineteenth leg did not touch the ground and is omitted. The movements of the head and antennae in the vertical plane is shown by the line 'ant.', and above are given two outlines of the animal at frames 41 and 71 showing the alternate positions of the head. The average duration of a pace by the more anterior legs when stepping evenly is 11 frames (0·74 sec.). The average duration of the forward swing is 6·8 frames (0·48 sec.), while that of the backward stroke is 4·2 frames (0·30 sec.). An average of 7 legs is in contact with the ground at once, see spots at frame 20 and elsewhere. The average phase difference between the more anterior legs is 0·2, see vertical line at frame 32. The average time interval between one leg being raised from the ground and the next being put in its place is 3½ frames (0·23 sec.), the average pace length by the more anterior legs is 6 mm.

All these records are of the same individual (Pl. **14** and text-fig. 2*a–c*.), the dimensions of which have been used for plotting the theoretical footprints shown in text-fig. 2*d–l*. This animal frequently omits to use one leg, which is then carried off the ground in a forward position; in text-figs. 3, 4, and 5A the right 6th leg is not used, and in text-fig. 5B the left 9th leg is stationary. The 9th leg steps normally in text-figs. 3, 4, and 5A, and the 6th leg was also used at other times. The general form of text-figs. 3–5 is the same as already described for text-fig. 1, p. 534. The movements of the right legs are shown by heavy lines in text-figs. 3 and 4, and those of the left legs by dotted lines; in text-fig. 5A and B the left leg movements are shown by heavy lines, and those of the right legs in text-fig. 5A by dotted lines. A time scale in seconds and in frames is given below, together with the body length 'B.L.' at one-second intervals, and the distances travelled by the head 'H.T.' and tail 'T.T.' ends of the body during each second, both to the nearest mm. The entries for 'H.T.' and 'T.T.' are the same only when the body length remains unchanged.

The phase relationship between legs of a pair varies at different times. There is a strong tendency for the legs of a pair to be moved in phase with one another (as seen by Moseley 1874, Haase 1889, and Kemp 1914), but they may exactly alternate, or show any intermediate condition. Pl. **15**, figs. 14 and 15 show the anterior five pairs of legs to be markedly out of phase, legs 9–14 in fig. 14 are approximately in phase, but legs 10–13 in fig. 15 are out of phase. Dr. Lawrence's photograph of a walking *Opisthopatus roseus* (1947, text-fig. 3) shows legs 1–4 and 10–11 to be approximately in phase with their fellows, while the remaining 12 pairs are markedly out of phase. The records of *P. sedgwicki* (text-figs. 3–5, show a greater degree of co-ordination between legs of a pair than is suggested by figs. 14 and 15. In text-fig. 3 most pairs of legs in starting to move do so almost in phase with one another; this correlation is maintained by the first pair throughout their uneven initial steps and after a steady rhythm has been set up during the last five paces. The 12th and 18th pairs also almost exactly maintain their co-ordination, but the other pairs lose and regain their similarity in an irregular manner. In text-fig. 4 the paired legs are seldom exactly in phase, and many move in alternate phase for a number of paces. In text-fig. 5A the first five pairs, performing a slow backstroke and a faster forward stroke, are almost exactly in phase. When the patterns of the gaits shown by the records are considered (see below), it is seen that the 'bottom gear' pattern with a relatively long backstroke (left half of text-fig. 3 and text-fig. 5A) is associated with paired legs in phase with each other. In the 'middle gear' pattern with equal forward and back strokes (text-fig. 4) the relationship is irregular. Few records have been obtained showing the legs of both sides of the body in a 'top gear' gait (with a relatively short backstroke), but these show the paired legs to be exactly out of phase (see fig. 12, Pl. **15**, where right legs 11 and 12 can be seen on the ground while their fellows are performing the recovery stroke). For further discussion see p. 553. There appears however to be a stronger correlation between the legs of one side of the body than between legs of a pair (see below). Whether an explanation for this lies in the structure of the nervous system is unknown. The paired ventral nerve cords lie far apart, just internal to the limb bases, while their cross connections in each segment are small, numerous and long. In *Geophilus* a variable relationship also exists between the legs of a pair, but the nerve cords are here close together as in other Chilopoda. Whether the connections between these nerve cords are more scanty than in other Chilopoda, as is suggested by the theoretical diagram by Holst (text-fig. 5, 1934), remains to be proved by an investigation into the fine structure of the nervous system.

Under favourable environmental conditions the same phase difference between legs of a pair may be present all along the body, and may persist for very many paces. The footprints recorded in Pl. **16**, fig. 20 show the sets formed by the left legs to be about 1/3rd of a pace in advance of those of the right. Four such sets are shown, and as

each is formed by 19 footprints, this phase difference must have been maintained for at least 23 paces. In fig 21 are seen the footprints made by legs which were approximately in phase with their fellows. Longer records showing such uniformity have been obtained, 35 or more paces by all the legs having been performed without change of phase relationships; this contrasts with the many fluctuations occurring on the cinematograph records.

On the left half of text-fig. 4 (0–6 secs.) *the phase difference between successive legs is fairly constant throughout the greater part of the body* *. Usually a complete step occupies 10 frames (0·71 sec.), and the forward and backward strokes are of equal duration. Each leg is about 3·5 frames (0·25 sec.) in advance of the leg in front, and its tip is put down on the ground about 1·5 frames after the leg in front is raised. A vertical line at frame 22 shows right legs 8 and 11 at the end of their forward strokes and three inter-segments lie between them. The other vertical lines on text-figs. 3–5 enable a ready recognition to be made of the phase differences. The value is a little over 0·4 for legs 1–3 at frame 137 on text-fig. 3, and for legs 16–18 at frame 39 on text-fig. 5A; it is about 0·3 for legs 2–5 at frame 134 on text-fig. 3; it is 0·25 for legs 1–5 at frame 66 and for legs 15–19 at frame 124 on text-fig. 3, and for legs 10–14 at frame 122 on text-fig. 4; it is 0·2 for legs 2–7 at frame 32 on text-fig. 5B; and about 0·16 for legs 8–14 at frame 73 on text-fig. 3. Thus a range of 0·45–0·16 may be taken as a usual phase difference between successive legs during moderately even stepping.

A line drawn through comparable positions of the left legs (dotted lines) on text-fig. 4 (see line 'r' text-fig. 1), would be approximately straight, showing no consistent curvature. The series of dotted lines is regular and uninfluenced by the inactive 6th right leg. A similar line drawn for the right legs (heavy lines) would fall in two parallel sections, one for legs 1–5, and the other for legs 7–19. The inactivity of the 6th right leg is associated with a retardation in the phases of the following legs. The movements of leg 7 fall exactly when one would expect those of an active 6th leg to take place (i.e. if the undulating line for leg 7 were transposed to the position of leg 6 it would form an even series with the lines for legs 1–5). Thus the right legs, excluding the 6th, step with an approximately even phase difference.

On the right half of text-fig. 3 the inactive 6th right leg is followed by the 7th leg performing a step of longer duration (13 frames) than legs 1–5 (10 frames), and this long step is repeated by right legs 8–10. The stepping of the left legs is uninfluenced by the inactive 6th right leg and by the unusual stepping of right legs 7–10. These two examples clearly indicate a dominance of the longitudinal co-ordination of the legs of one side over the transverse co-ordination between legs of a pair, another example is given on p. 550. A conflict between these two co-ordinations is perhaps shown by the 6th left leg on text-fig. 3. There is at first a tendency for the 6th right leg to step in phase with its fellow, but it becomes inactive at frame 66. The 6th left leg takes one appropriate step alone (frames 51–84), and then remains in a forward position missing one pace (frames 84–94) before stepping appropriately with the other left legs.

Phase differences which are fairly uniform along the body are also shown by figs. 10 and 11, Pl. **15**, for *P. moseleyi*, and by Dr. Lawrence's photograph of *O. roseus* (1947). In the former about 8 cycles of leg movement are seen along the series of 21 legs, and 7 cycles are seen along the 18 legs of *O. roseus*, while in text-fig. 4 (left half) 6 cycles are seen along the 19 legs. The phase difference in these photographs is about 0·4, and on the left half of text-fig. 4 it is usually about 0·35. Each cycle of limb movement is transmitted forwards along the body in a little over 4 secs. on the left half of text-fig. 4. In the animal shown in Pl. **15**, fig. 11, the rate of forward transmission is slower as the phase difference is greater. If

* The initial irregularities of the last few legs is associated with a straightening of the tail end of the body, see outlines shown above.

0·45–0·16 represents the range of phase differences between successive legs, then the times taken by a cycle of limb movements to be transmitted along the body of *P. wedgwicki* lies between 6 and 2 secs.

At other times *the phase difference is small anteriorly and increases progressively along the body*, instead of showing the uniformity just described. This is seen very clearly in a photograph of a walking *P. moseleyi* by Holliday (1942, pl. vi, fig. 3), where the phase difference is approximately 0·2 between legs 4–9, 0·25 between legs 9–13, 0·33 between legs 13–16, and approaching 0·5 between legs 16–20. A less even range of phase differences is seen in text-fig. 5A near frame 25, where the vertical lines mark regions with approximate phase differences of 0·2 between legs 1–6, 0·25 between legs 6–10, almost 0·5 between legs 11–13, 0·33 between legs 13–16, and 0·35 between legs 16 and 18. If the stepping here had been as orderly as in Holliday's photograph, a line joining comparable positions of each leg ('r' on text-fig. 1) would be curved with the steeper slope lying across the more anterior legs.

Since alterations of phase difference between successive legs do not alter the speed of progression (p. 536), a transition between a state of uniform phase difference and the one described above would not appear to be mechanically difficult. A small phase difference is associated with slow gaits (text-fig. 3, frame 73, legs 8–14, and text-fig. 5A, frame 25, legs 1–6), and also with fast (text-fig. 5B, frame 32, legs 2–7), see below, and with certain types of irregular movement, pp. 550 and 555. An alteration in the phase difference at various times is associated with a change of gait (see p. 553).

Of the five possible *patterns of gait* described above for text-fig. 1, four can be seen on the cinematograph records. Gait A with equal forward and backward strokes (5 : 5) and a large phase difference between successive legs (0·3–0·45) is frequent, as on the left half of text-fig. 4 and on the right side of text-fig. 3. This is the gait observed and drawn by Lankester (1904) for *P. capensis* showing his 'swing-group' number of two legs. Gait D with equal forward and backward strokes (5 : 5) and a small phase difference is only of momentary occurrence, it is approached by legs 15–19 on the right half of text-fig. 3 but the phase difference is larger (0·25) than on text-fig. 1. The duration of the pace by gaits A and D is usually 10 frames (0·71 sec.). Gait E with a long forward swing and a short backward stroke and a small phase difference (about 0·2) is shown irregularly by the majority of legs on text-fig. 5B, and most clearly by legs 2–8 on the left half of the figure. This is the gait observed by Kemp (1914) to be associated with hurried locomotion (see p. 552). Gait B with a large phase difference and relatively shorter backstroke does not occur on the records (see also p. 556). Gait F with a short forward stroke and a long backstroke and a small phase difference is shown by legs 8–18 on the left 2/3rds of text-fig. 3, and by legs 1–9 on text-fig. 5A. Gaits E and F show various pace durations which usually exceed those shown by gaits A and D, and frequently range between 11 and 15 frames (0·67–0·94 sec.). The left half of text-fig. 4 shows a fairly even performance of gait A by all the left legs. It is believed that the animal is capable of carrying out gaits E and F with equal uniformity when unharassed by the stimulus of bright light, but gait F is probably not maintained for long (pp. 550–553).

Some *types of irregular stepping* will be noted before a further consideration of the gaits. The former are of localized occurrence, and presumably cannot be performed evenly throughout the body. A pace of abnormally long duration, and with equal forward and backward strokes, may be repeated by one or two of the immediately posterior legs of the same side at a large phase difference. Such steps are marked K in text-figs. 3 and 5A.

Another type of pace of long duration is formed when a leg swings forward slowly and steps back normally. During the forward movement one or two paces performed by the more anterior legs are missed out, and on the backstroke the foot is put down appropriately in a set of footprints. This type of abnormal step is usually propagated along the remainder of series of legs of that side, and the succeeding step by all legs may or may not be normal. Such long steps are marked in text-fig. 4, starting at G, H and J for right legs and at W, X, Y and Z for left legs. At G the legs miss out two paces and at W, X and Z they omit one pace, at Y the step is of abnormal duration, but being the first leg it cannot be said to miss out a step taken by a leg in front. The slow step at H appears to be called forth by the previous irregularities of legs 6 and 7, and perhaps also of legs 8 and 9. It is again clear that a longitudinal co-ordination between legs of one side is stronger than a transverse co-ordination between legs of a pair (p. 548), as all these abnormal paces are propagated posteriorly quite independently (the footprints of these paces are shown on text-fig. 8 and described on p. 560). There is no mechanical hindrance to the stepping of a leg following one performing the slow pace just described, an exceptional case of such a step being taken is shown by right leg 10 at frame 109–119, in text-fig. 4. The hindrance appears to be a nervous one, each leg swinging forwards until the leg before it has vacated a set of footprints which is then occupied. The legs are always put down appropriately in a set of footprints and not in between them. The completion of a step by the leg immediately in front is not always a necessary factor for the calling forth of a step. The completion of a step by the nearest active leg appears to be sufficient. A possible reason for this type of long step is given on p. 555.

The duration of the pace and of the backstroke, the angle of swing of the legs and the resultant speeds achieved by the various gaits will now be considered. In table I are given particulars of gaits of patterns A–E, calculated for pace durations of 10, 11 and 12 frames, and with backstrokes of different durations (3·5–7·5 frames). The angles of swing of the leg are given by the values for θ (see p. 542), and the same values for θ in different gaits indicate that the angles of swing * of the legs are respectively the same. It is seen that an increase in the angle of swing of the leg at the same duration of the pace results in an increase in the speed for each pattern of gait, and that for each pattern of gait and angle of swing of the leg an increase in the pace duration results in a decrease in the speed (see entries on the same horizontal level in columns I–III.

In text-fig 4 most steps, other than the abnormally long ones, are of the *A pattern* (5 : 5) and duration of 10 frames, and the speed achieved ranges from 6–10 mm. per sec. (excluding the period 0–2 secs. occupied by a straightening of the tail end ; the abnormally long paces which omit steps will be disregarded as they are unlikely to effect the speed). This means that the angles of swing of the legs varies between values of slightly less than '$\theta_{2\cdot5}$' to '$\theta_{3\cdot5}$', and that gaits 'A, $\theta_{2\cdot5}$'–'A, $\theta_{3\cdot5}$' (table I column I) cover the range of movement shown in text-fig. 4. The speed of the tail end in the middle of text-fig. 4 (p. 2–8) is 8 mm. per sec. This corresponds with gait A, $\theta_{2\cdot8}$ which has a 'd' value of 3·4 mm. (table I column I). It is satisfactory to find that the sets of footprints recorded at the same time (text-fig. 8 and Pl. **16**, fig. 17) correspond with the theoretical pattern drawn for a 'd' of 3·4 mm., at a moderate extension of the body (66–68 mm.), shown by text-fig. 2*e*, interrupted line (see also p. 553).

Gaits of the *F pattern* approximately (3·5 : 6·5) and frequently of 11–13 frames duration, are seen on the left half of text-figs. 3 and 5A, and are associated with lower speeds of 4–6 mm. per sec. Table I shows gaits of F, $\theta_{2\cdot5}$ F, $\theta_{2\cdot8}$ and F, $\theta_{3\cdot2}$ at pace durations of 11, and 12 frames to have speeds between 4·6 and 6·4 mm. per sec. which are comparable with the direct records. Thus the angles of swing of the legs performing the slower gaits F are much the same as for the faster gaits A.

* Factor 'θ' will be referred to briefly as 'the angle of swing', although this is an incomplete definition, see pp. 533 and 542.

When starting to walk (text-fig. 3) the animal's momentum increases, and presumably the leg muscles cannot perform the backstroke as quickly to start with as they can when a steady speed has been reached (text-fig. 4), and thus gait F is probably a muscular necessity in starting up or gaining speed. Once momentum is acquired, the duration of the backstroke can be decreased from about 9 frames (0·6 sec.) to 5 frames (0·35 sec.), and gait A can then be performed (right side of text-fig. 3), see also p. 553.

Gaits of *pattern E* (6·5 : 3·5) seen in text-fig. 5B are associated with a longer duration of the pace than in gaits A, and show speeds of 7–9 mm. per sec. Their characteristics are in agreement with the entries for gaits E in table I, columns II and III which are not shown in italics. The force exerted by different legs is probably not identical as their sizes vary. However, the same leg performing different gaits which result in the same speed will not exert the same force if the gaits have different numbers of legs on the ground at one moment. It is shown below that gaits E, A and F have about 7, 10 and 13 legs respectively on the ground at once. The absence from the records of speeds above 9 mm. per sec. for gait E, while 10 mm. per sec. is shown on one occasion for gait A, indicates the upper limit of the muscular power which a leg can exert. Gaits of the E pattern which are not present on the cinematograph records are shown in italics and within brackets in table I. they are all fast gaits, which must be absent from the cinematograph records because a leg cannot provide the necessary force for their execution, and in fact cannot execute a backstroke through the given angles of swing in the time indicated in the table. A maximum effort put out by the animal in the A gait gives a slightly greater speed than the maximum performance of an E gait, because the 10 legs which are propulsive at one moment out of the total 19 can execute the backstroke through a greater angle of swing than can be done by the 7 propulsive legs in the E gait. The gaits shown in table I in italics alone are doubtfully possible to the animal (see also p. 555).

In table I nine *durations of the backstroke* are considered, ranging from 3·5–7·5 frames (0·53–0·25 sec.) at intervals of 0·5 frame (1·28 sec.). There is a limit to the possible shortening of the duration of backstroke if the angle of swing of the leg remains the same (see above.) It appears to be impossible to carry out the backstroke in 0·21 sec. (3 frames as in text-fig. 1 for gaits B and E) at any angles of swing between $\theta_{2\cdot5}$ and $\theta_{3\cdot5}$ although smaller angles may be possible. A backstroke of 0·25 sec. (3·5 frames) is doubtfully possible at $\theta_{2\cdot5}$, and impossible at greater angles (gait E); a backstroke of 0·28 sec. (4 frames) is possible at $\theta_{2\cdot5}$ (gait E), one of 0·32 sec. (4·5 frames) is possible at $\theta_{2\cdot5-2\cdot8}$ (gait E), and one of 0·35 sec. (5 frames) can perform angles of $\theta_{2\cdot5-3\cdot5}$ (gait A). Each leg in gait E bears a greater load than in gait A, since fewer legs are in contact with the ground at once in gait E (see below). Greatest speeds are thus performed by gaits of the A pattern at a maximum angle of swing of the leg (backstroke of 0·35 sec. and $\theta_{3\cdot5}$), and by gaits of the E pattern at a longer duration of the pace but a shorter backstroke, and a smaller angle of swing of the leg (backstroke of 0·28–0·32 sec. and $\theta_{2\cdot5-2\cdot8}$).

The *degrees of extension of the body* are shown in text-figs. 3–5 ('L.B.'). The longer body extensions (75–73 mm.) are associated with gaits of the E pattern (text-fig. 5B), the shorter extensions (58–59 mm.) with gaits of the F pattern (text-figs. 3 and 5A), and the moderate extensions (67–69 mm.) with gaits of the A pattern (text-figs. 3 and 4). There appears to be a general correlation between the speeds and the degrees of extension of the body. The distances travelled by the head and tail ends of the body during every second have been measured for 9 cinematograph records of the same animal. For 19 periods of one second the body length remained constant, 38 such periods show a changing body length, and at no time did the extension remain unchanged for more than 3 seconds. Therefore stepping cannot have been uniform through many of the measured periods. The speeds achieved by several groups of extensions of this animal are shown below, excepting the single record of 10 mm. per sec. at extension 68 mm. seen in text-fig. 4. No extensions of 60–64 mm.

were recorded other than those in starting up, as seen in text-fig. 3. Table II shows that the faster speeds are correlated with the longer extensions of the body, which, as has already been noted, are associated with gaits of the E pattern. When the body extension steadily decreases so does the speed (text-fig. 5B), and the converse is shown by a record where the extension increases from 68–72 mm. over a period of 7 secs., while the speed accelerates from 6–8 mm. per sec. However in text-fig. 4 an irregular increase of speed from 7–10 mm per sec. is associated with an increase in the

TABLE II.

Longitudinal extension of the Body in mm	Speed in mm. per sec.
73–75	7–9
71–72	6–9
68–70	6–8
66–67	5–7
58–59	4–7

angle of swing of the leg rather than a change in the pattern of the gait, and the alteration in extension of the body is small. The degree of extension of the body must be associated with the muscular mechanism, which presumably can most easily carry out a backstroke of short duration (0·28–0·32 sec.) at a maximum extension of the body, and a backstroke of long duration (0·50–0·53 sec.) at a short extension, and an intermediate backstroke (0·35 sec.) at an intermediate body extension, the angle of swing of the leg remaining the same.

The *number of legs in contact with the ground, and their disposition*, at one moment varies in the different gaits, and in text-figs. 3–5 spots below the heavy lines mark the legs of one side of the body which touch the ground at that moment. In gaits A and D where half the legs of the animal are propulsive at one moment, 10 out of the 19 legs are shown by the spots to be on the ground at frame 49 on text-fig. 4 and frame 111 on text-fig. 3. In gait F where about 2/3rds of the pace duration is occupied by the backstroke 2/3rds of the legs will be propulsive, and 13 legs are shown by the spots to be on the ground at frame 84 on text-fig. 3, and 12 legs at frame 20 on text-fig. 5A. In gait E where about 1/3rd of the pace duration is occupied by the backstroke, 1/3rd of the legs will be propulsive, and 7 legs are shown by the spots at frames 20, 41 and 71 on text-fig. 5B. Thus in the fast gait E there are fewest points of contact with the ground, and in the slow gait F their number is greatest. A general similarity is here shown to the locomotion of tetrapods, where the number of points of contact with the ground decreases with increasing speed. (See also Appendix I).

Kemp (1914) noted that in more hurried as opposed to slower locomotion 4 or 5 adjacent pairs of legs 'act together' so that the body is only in contact with the ground in a few places. The correlation between speed and the number of contacts with the ground is not exact. The speed of a trot may exceed that of a canter in tetrapods, and in Peripatus the speed of gait A may exceed that of gait E. Gait A, $\theta_{3\cdot5}$ has a moderate body extension, and a speed of 10 mm. per sec. and is as fast or faster than gait E, $\theta_{2\cdot5}$ (column I table I) or E, $\theta_{2\cdot8}$ (column III), both with a maximum body extension, yet gait A has more legs on the ground than gait E. However table II shows that the animal usually employs gait E (showing the longer body extensions) for the faster speeds. Since this gait shows the fewest contacts with the ground at one moment, and also the shortest duration of the backstroke and a slightly longer duration of the pace, each leg will spend a smaller proportion of its time in an actively propulsive state than at any other gait. Conversely in gait F each leg will spend a maximum proportion of its time in a propulsive state.

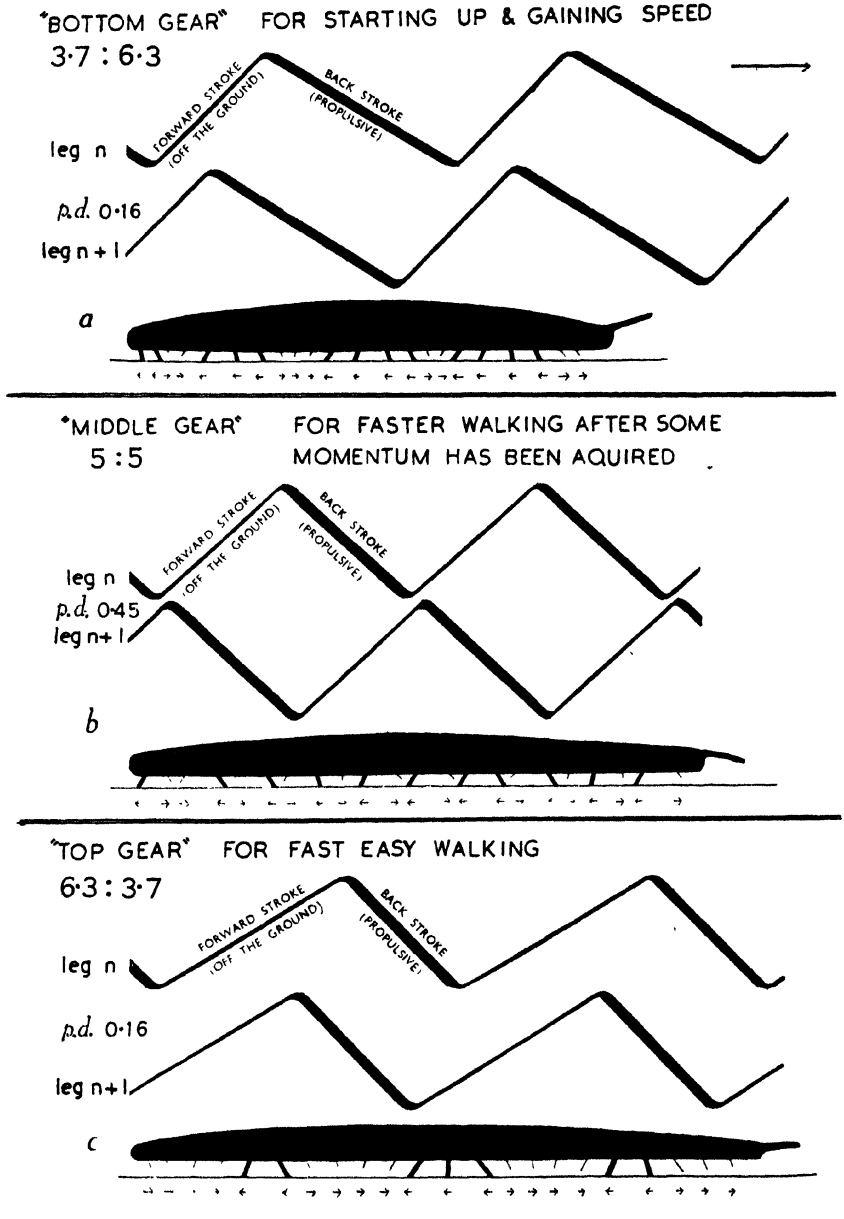
The phase relationship between legs of a pair is correlated with the gait (see p. 547) In starting to walk the legs of each pair become propulsive successively as the body elongates (text-fig. 3), and an even pull will be exerted by the united efforts of each pair. Even when the whole body is in motion, the employment of an F gait (with many propulsive legs at one moment), will be facilitated by an even pull being exerted by both legs of a pair An E gait, however, with few points of support from the ground, results in several successive segments being unsupported directly If the paired legs are in opposite phase, sections of the body which are unsupported by their legs on one side will be supported by one or more propulsive legs on the other side, and this disposition clearly must be advantageous. The fluctuations of the relationship between legs of a pair in the A gait (text-fig 4 and right half of text-fig. 3) must be the consequence of the employment of a gait intermediate between the above extremes in which the paired legs are regularly moved neither in nor out of phase with each other It is of interest to find that in the land Arthropoda with many legs (see Part II), those animals which employ a gait comparable to the F gait also move their paired legs in phase with each other, while those which employ gaits comparable to the E gait move their paired legs in opposite phase

The gaits of Peripatus

We can thus go further in an *analysis of the movements* of the animal of mean length 66 mm. recorded by the films, and also give an explanation for the occurrence of the uniform or the changing phase difference between successive legs (pp. 548 and 549) The slowest speeds, which alone are practicable when starting to walk, were performed by a gait of the F pattern (approximately 3·7 : 6·3), with a long pace duration, a small or moderate angle of swing of the leg, a small phase difference (0·16), a small extension of the body and legs, more than half of the legs in contact with the ground at once, and legs of a pair approximately in phase with each other Moderate speeds, and on one occasion a maximum speed, were performed by a gait of A pattern (5 : 5), with a shorter pace duration, a moderate or maximum angle of swing of the leg, a larger phase difference (0·45), a moderate extension of the body and legs, half of the legs in contact with the ground at once, and legs of a pair in variable phase relationship with each other The faster speeds were usually performed by a gait of the E pattern (approximately 6·3 : 3·7), with a long pace duration, a moderate angle of swing of the leg, a smaller phase difference (0·16–0·2), a maximum extension of the body and legs less than half of the legs in contact with the ground at once, and legs of a pair approximately out of phase with each other

Gait F (approximately 3·7 : 6·3) is employed as a '*bottom gear*' for supplying a maximum effort towards gaining momentum. It gives speeds of 4·6–6·4 mm. per sec. (see gaits F, $\theta_{2\cdot5-3\cdot2}$ in columns II and III of table I) As the speed increases it becomes possible for the animal to reduce the duration of the backstroke which will reduce the number of legs in contact with the ground, and the phase difference increases to a maximum so that the propulsive legs are evenly distributed . gait F is thus transformed into gait A. This is clearly seen in text-fig. 3 where the anterior legs (1–3), which have been stepping for longer, have achieved gait A on the right side of the figure, while the posterior legs (15–19) have shortened the backstroke but have not yet increased the phase difference greatly (see the vertical line at frame 124). Thus a phase difference which is larger at the anterior end of the body than at the posterior is associated with an alteration of the gait and an increase in speed.

Gait A (5 : 5) constitutes the '*middle gear*', with equal forward and backward strokes, and gives speeds of 7–9 mm. per sec. (see gaits A, $\theta_{2\cdot5-3\cdot2}$ in column I of table I). The animal can either maintain this speed at the same gait, or it can accelerate by increasing the angle of swing of the leg to a maximum achieving 10 mm. per sec. (see gait A, $\theta_{3\cdot5}$ in column I of table I), in either case continuing to use half of its legs in a propulsive manner at once. Alternatively it can maintain a fast speed with less than half of its legs on the ground at once by decreasing the duration of the



TEXT-FIG. 6.

[*For legend see p.* 555.

backstroke and slightly increasing the pace duration, so lengthening the rest period of each leg, and at the same time decreasing the phase difference, which will minimize stumbling, as gait A is transformed into gait E.

Gait E (approximately 6·3 : 3·7) is employed as a '*top gear*' which can only be used after sufficient speed has been acquired by the use of the 'bottom' and 'middle gear' gaits. It gives speeds of 7·8–8·7 mm per sec. (see gaits E, $\theta_{2\cdot5-2\cdot8}$ in columns II and III of table I). The maximum angles of swing of the leg are impracticable in this gait as each leg carries a greater load than in 'middle gear' (see E gaits in italics in table I). If the animal changes its gait to a fast easy walk in this manner at the anterior end of the body first, it will show a smaller phase difference anteriorly than posteriorly, and also a considerable degree of anterior extension of the body, as is seen in Holliday's photograph referred to on p. 549. A change to 'bottom gear' anteriorly would give the same disposition of the phase differences along the body, but would be accompanied by a slight longitudinal contraction at the anterior end. These conclusions are summarized in text-fig. 6, in which the heavy lines depict the legs in the propulsive phase and the thin lines those in the forward swing. The direction of movement of each limb in the silhouettes is indicated by the arrow below it. The disposition of the legs shown represents the calculated positions at one moment in each gait, and can be compared with the photographs of the animal (Pl. **15**, and see below).

Since easy fast walking is associated with a long rest period for each leg, the occurrence of the long forward strokes which miss out one or two footfalls on text-figs. 4 and 5 G–J and W–Z (see p. 550) may be associated with a tendency to walk fast under the stimulating bright light. Such paces are absent from the records showing starting up and slow walking (text-figs. 3 and 5A). Certain Myriapoda have elaborated a type of stepping associated with fast moving (see Part II, *Lithobius*, etc.) in which one or more footfalls of the preceding legs are overstepped, but the procedure is not quite the same as in these paces of Peripatus.

The gaits shown by the cinematograph records to be either impracticable or of limited usefulness are of interest. Only gait C with a backstroke of relatively long duration and a large phase difference is mechanically difficult or impossible at anything but small angles of swing of the legs, and it has not been recorded.

The D gait has only been recorded locally on the body during a transition from an F to an A gait (see above and text-fig. 3, frame 124); it is not maintained, the animal favouring an A rather than a D gait for uniform walking with equal forward and backward strokes. In both gaits half of the legs are in contact with the ground at once, but their disposition is different. In an A gait of phase difference 0·45, approximately every other leg is on the ground (text-fig. 6*b*) while in a D gait of phase difference 0·15 groups of three or four successive legs are either on or off the ground (text-fig. 9*b*): the latter condition must impose greater and more uneven strains on the body musculature than the former. In the Myriapoda the D gait is habitually performed by *Polydesmus* (see Part II), where the exoskeleton is doubtless

TEXT-FIG. 6

A summary of the analysis of the locomotory movements of *Peripatopsis* showing the three gaits most frequently employed. The movements relative to the body of two successive legs are shown by the thin and thick lines in respect of time. Silhouettes of the same animal are drawn with the observed body proportions at each gait, and the positions of the legs are those calculated for a regular performance of the three gaits. Legs executing the propulsive backstroke are shown by heavy lines and those in the recovery swing are shown by thin lines. Arrows below each leg shows their directions of movement.

Fig. 6*a*. The duration of the forward and backward strokes are as (3·7 : 6·3) the phase difference between successive legs is 0·16, and the duration of the pace is 0·84 sec.

Fig. 6*b*. The duration of the forward and backward strokes are as (5 : 5), the phase difference between successive legs is 0·45, and the duration of the pace 0·7 sec.

Fig. 6*c*. The duration of the forward and backward strokes is as (6·3 : 3·7), the phase difference between successive legs is 0·16 and the duration of the pace 0·84 sec. This is an extreme gait, more usually the phase difference is about ·2 as in fig. 9*c*.

better able to withstand the uneven strains imposed by this gait. Thus the almost complete absence of the D gait in Peripatus must be due to the unsuitability of this gait for a soft skinned animal.

The B gait with a backstroke of relatively short duration and a large phase difference is not performed by Peripatus. The reason for its absence is less clear than for the D gait. The disposition of the legs in a B gait at all moments is as shown in text-fig. 9*d*. An exactly similar disposition of the legs is found at one moment during each pace in an A gait at a phase difference of 0·4, although at other moments this A gait (text-fig. 9*a*) shows almost the same disposition of legs at does an A gait at a phase difference of 0·45 (text-fig. 6*b*.). An awkward strain on the soft body wall might occur in this gait, since the stiff-bodied Myriapoda perform gaits with backstrokes of as short or even shorter relative durations and at large phase differences. However, the nature of such strains cannot be profitably discussed until more is known of the muscular systems. A tendency to increase the phase difference in a fast gait with a relatively short duration of the backstroke will enable an animal to use the same footprints (see Part II). This tendency is strongly developed in the Chilopoda but not in Peripatus. On the other hand the existence of a small phase difference in such a gait will minimize the possibility of stumbling by uneven stepping (gait E), and appears to be the more serviceable to Peripatus when walking rapidly over rough ground.

The animals shown in Pl. **15** were photographed with 'photoflood' instantaneous illumination, and may thus represent more normal and regular stepping than the records of the cinematograph camera. No simultaneous records were made of the speeds, but the gaits in figs. 10–13 can be clearly diagnosed. The animal in fig. 11, with almost every other leg on the ground, closely corresponds with the theoretical figure for gait A at a phase difference of 0·45 (text-figure 6*b*), while fig. 12 with more legs off the ground a 10% greater extension of the body, and a smaller phase difference corresponds with fig. 9*c* representing gait E at a phase difference of 0·2. The speed in fig. 12 was probably greater than in fig. 11 since the angle of swing of the legs in fig. 11 is not remarkedly greater than in fig. 12. In the other animal shown in fig. 13 it is not easy to see how many legs are in contact with the ground, but they appear to be many; the phase difference is small, the angle of swing of the legs is less than in fig. 10 and the extension of the body is 17% less than in fig. 10, so that this animal must have been moving slowly by gait F in fig. 13 (compare with text-fig. 6*a*) and faster by gait A at a phase difference of 0·4 in fig. 10 (compare with text-fig. 9*a*).

The records of the Footprints.

It has been shown above (p. 536 and text-fig. 2) that the tracks formed by an animal consist of paired sets of footprints, the pattern of each set being determined by the distance 'd' and the dimensions of the animal at the particular degree of extension. A different pattern results from every change in either 'd' or in body length or in both. The frequency of repetition of the sets to form the track is determined by the length of the stride. Different gaits with the same value for 'd' may or may not have the same stride lengths, and the shape of the sets made by such gaits will be identical only when the body length is the same. Since the extension of the body usually changes with alterations in the gait, and since an alteration of the angle of swing of the leg changes the value of 'd', markedly different gaits will never form identical tracks.

The tracks made on smoked paper by a *P. sedgwicki* about 50 mm. long are shown in figs. 18–25, Pls. **16** and **17**, the direction of walking being given by the arrows. The right half of the track is frequently obscured by a leg having been dragged over the ground, and the left half of the track will be mainly considered. In figs. 18–23 the animal was walking in an approximately straight line, while in fig. 25 it was turning to the left. Only in figs. 24 and 25 were the paired terminal claws used. The persistent regularity of stepping by the animal when forming these tracks under a dim light has been noted (p. 547).

The general form of the tracks will first be considered and then the gait which must have formed each record will be deduced. The sets are compact in figs. 20 and 21, at the bottom of figs. 19 and 22 they are α-shaped; in fig. 19 they become progressively more elongated, joining each other at paces 4–6 (the footprints of the posterior legs in the 5th and 6th sets are not clear); in fig. 18 the sets are longer still and overlap considerably in a forward direction; the overlap in fig. 23 is so great as to render the component sets unrecognizable; and in fig. 25 the sets overlap backwards.

The length of the stride has been shown to be correlated both with the speed and with the duration of the pace, and is only roughly proportional to the speed alone (p. 542). The stride lengths of either leg 1 or of all the legs in figs. 18, 22, 20, 19, 21 and 25 are 4·1, 3·4, 3·4–3·1, 3·1, 2·9–2·5, and 2·2 mm. respectively, so that the animal was possibly walking fastest when making the record of fig. 18 and progressively slower in the other records in the order mentioned. The speed in fig. 19 altered during the recording. The lengths of the paces by leg 1 are almost uniform at 3·07 mm., but the step between the 2nd and 3rd set is 0·26 mm. longer and is compensated for by the following step being 0·19 mm. shorter, so that the speed was probably uniform when the head end of the animal passed over the record. The pace lengths of the middle and posterior legs on this record increase, so altering the pattern of the sets, and indicate that an increase in the speed began after the head end had passed over.

In fig. 22 the pace length and the antero-posterior extension of each set is uniform, but the 1st and 6th sets are more compact in the transverse direction than are sets 2–5, which progressively widen, so that in set 5 the more posterior footprints no longer cross over the more anterior ones (the first leg has left no clear mark on sets 4–6). This must be due to a slight and temporary bearing of the animal to the left, so that the footfalls were progressively displaced to the left. The alteration of direction was very slight, as the subsequent track is straight and almost in line with the portion shown.

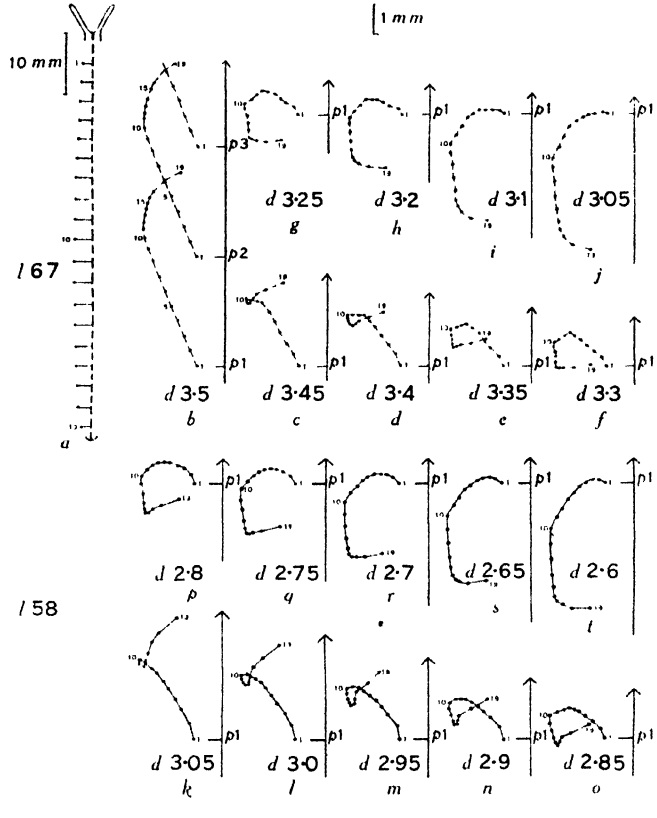
Fig. 25 shows the tracks made during a more pronounced turn to the left. The footprints are spread more laterally by a displacement of the body. The ends of the sets formed by the more posterior legs are obscured by their overlap of the next posterior set (see the shape of the sets shown in text-fig. 7*g–j*). The three sets at the upper end of the record show the footprints and claw marks more laterally displaced by a more rapid turning movement of the body. The speed is slower than in the records which show walking in an approximately straight line.

The width of the track in figs. 23, 18, 22, 19, 20, and 21 is about 5·1, 5·05, 5·1, 4·87, 4·7 and 4·4 mm. respectively. This width is determined by the distance between the tips of the limbs, and this depends upon the degree of extension of the body and legs, being narrower for the shorter extensions which accompany the slower speeds, but the relationship may not be exact (p. 533). The relative speeds of figs. 19–22 implied by the width of the track are not quite the same as those roughly indicated by the stride lengths, the track is slightly narrower in fig. 20 than in fig. 19 while the stride length in fig. 20 is greater (see also below), but the relative speeds for the other figures implied by both the width of the track and by the length of the stride are the same (see p. 560).

The animal unfortunately was not photographed, but text-fig. 7 shows the proportions of a fictitious animal, and its calculated sets of footprints, at a variety of values of 'd' for a moderate and a short extension of the body, which must closely correspond with the animal which formed the footprints. Text-fig. 7*b* was made from a tracing of the sets shown in fig. 18 on to which the probable positions of each footprint were inserted, and the proportions of the animal shown in fig. 7*a* were deduced from text-fig. 7*b*.

The details of the gaits which formed each of the records shown in figs. 18–22 can be deduced from the length of the stride, the value of 'd', which can be estimated by comparison of the records with the sets of footprints shown in fig. 7, and a fuller

table I (which is not shown here). Alternative values of 'd' may be taken giving the same general pattern of the footprints at different body extensions when the pattern cannot be matched with sufficient accuracy. The manner of calculation of the gaits is given in Appendix II.



TEXT-FIG. 7.

Fig. 7*a* shows the dimensions of an animal reconstructed from the footprints seen in fig. 17, Pl. 16, and scaled to a length of 67 mm. so that direct comparison may be made with the animal 67 mm. long shown in text-fig. 2*b*. An animal of the proportions shown in fig. 7*a*, but of smaller size, must have made the footprints recorded in figs. 18–25, Pls. 16 and 17.

Figs. 7*b–t* show the calculated sets of left footprints which will be formed at various values of 'd' (the distance travelled in time 't', see text-fig. 1) for two extensions of the body. A moderate extension of 67 mm. '*l*67' will give sets as in figs. *b–j*, and a short extension of 58 mm. '*l*58' will give sets as in figs. *k–t*. The scale and the conventions are the same as in text-fig. 2. The footprints of leg 1 at pace 1 'p.1' are placed at the same transverse levels for figs. *b–f*, *g–j*, *k–o*, and *p–t*; the second and third paces are shown only in fig. *b*. In fig. *b* the sets overlap forwards, in figs. *c–g* and *l–q* they will be separate, and in figs. *i–j* and *s–t* they will overlap backwards. These patterns closely resemble some of the actual records in figs. 18–20, 22, and 25, Pls. 16 and 17, where similar sets of footprints left are marked on the left by similar values for 'd' at the body extension indicated.

Fig. 18 will be considered first. The stride length indicates that the speed was greater than in figs. 19–22, and so the extension of the body was likely to have been moderate or great. Sets of footprints resembling those given by a 'd' of 3·5 mm. at a moderate body extension (text-fig. 7*b*) are seen throughout the record (leg 19 does not appear to touch the ground, a frequent occurrence for the short legs at the faster

speeds (The calculated gait which could give these tracks is (A, 0·36)$\theta_{2\cdot7}$ (see Appendix II) at a speed of 7·7 mm. per sec. for an animal of mean length 66 mm., where the figure within the bracket indicates the phase difference between successive legs. The A gaits on the cinematograph records (text-fig. 4 etc.) show phase differences of 0·3–0·45, and gaits with equal forward and backward strokes rarely show lower values. Thus a gait with a phase difference of 0·36 comes within the range of the A pattern of gait. The tracks could not have been made by an E gait at a markedly greater extension of the body or the phase difference would be much less and the speed greater. Fuller reasons against an E gait being possible here are similar to those given below concerning the impracticability of an E gait for fig. 22.

Fig. 22. Two alternative values of 'd' must be considered. If the body was at a moderate extension the 'd' must have been about 3·35 mm. (text-fig. 7*e*), and if the extension was short the 'd' must have been 2·9 mm. (text-fig. 7*n*); if the extension was intermediate, then the 'd' and also the exact pattern of the footprints must have been intermediate The calculated gaits (see Appendix II) which could give these tracks are the intermediates between (A–D, 0·28)$\theta_{2\cdot3}$ and (C–F, 0·36)$\theta_{3\cdot3}$ at speeds of 6·5–5·4 mm. per sec. for an animal of mean length 66 mm. The former gait is about half way between an A and D pattern and the latter is practically a C gait. Only a limited number of these theoretical gaits are practicable. A gait of the C pattern with a large phase difference and a large angle of swing of the leg does not occur, and a gait with equal forward and backward strokes (A–D) will usually be found with a large phase difference The practicable gaits lie in between these two impracticable extremes, and as an intermediate phase difference must be $>$0·28 and $<$0·36 the gait must be nearer to the A pattern than to the C–F types. Thus the actual gait which must have formed the tracks is almost of the A pattern, but with a backstroke slightly longer than the forward stroke: the angle of swing of the leg is $>\theta_{2\cdot3}$ and much less than $\theta_{3\cdot3}$; the duration of the pace is a little longer than for fig. 18 (about 0·78 sec., see column I, table I); and the extension of the body is moderate. The resultant speed will be nearer 6·5 than 5·4 mm. per sec. for an animal of mean length 66 mm

Fig. 19. There are similarly two alternative values of 'd' (see text-fig. 7*e* and *n*) and two theoretical extremes between which all gaits give the same pace length, these are (C–F, 0·27)$\theta_{2\cdot6}$ at a long pace duration (column III), and (A–D, 0·19)$\theta_{2\cdot0}$ at a short duration of the pace (column I), giving speeds of 4·9 and 5·7 mm. per sec. respectively by an animal of mean length 66 mm. (see Appendix II). A gait (C–F) with as large a phase difference as 0·27 is not frequent, nor is an (A–D) gait with as low a value as 0·19. The practicable intermediate gaits have a phase difference $>$0·19 and $<$0·27, that is further removed from the A pattern than is the gait giving fig. 22, but not near to an F gait; the backstroke is a little longer than the forward stroke, and a little longer than for fig. 22; the angle of swing of the leg is $<\theta_{2\cdot6}$ and $>\theta_{2\cdot0}$, probably slightly less than for fig. 22; the duration of the pace is a little greater than in fig. 22 (0·78–0·86 sec., columns II and III), and the extension of the body is slightly less than for fig. 22. The resultant speed will be about mid-way between the above mentioned extremes for an animal of mean length 66 mm.

Fig. 20. Two alternative values of 'd' are indicated by the stride length and by text-fig. 7*f* and *o*, giving two theoretically extreme gaits (A–D, 0·29)$\theta_{2\cdot3}$ with a short pace duration (column I), and (C–F, 0·38)$\theta_{3\cdot3}$ with a long pace duration (column III), giving speeds of 6·5 and 5·4 mm. per sec. respectively by an animal of mean length 66 mm. (see Appendix II). Both of these gaits are impracticable for the reasons given above for the gaits concerning fig. 22, and the practicable intermediates have a phase difference of $>$0·29 and $<$0·38, that is almost an A pattern and far removed from the C–F patterns; the backstroke is slightly longer than the forward stroke, but of shorter duration than for fig. 22; the angle of swing of the leg is $>\theta_{2\cdot3}$ but far removed fron $\theta_{3\cdot3}$; the duration of the pace is slightly less than for fig. 22 and greater than for fig. 19; and the extension of the body is moderate. Since the width of the track is less than in fig. 22 the body may have been shorter, and therefore the speed may have been slightly less than in fig. 22.

Fig. 21. Only one value for 'd' is indicated by the stride length and by text-fig. 7*o–p*, and the gait possessing the required features is (C–F, 0·23)$\theta_{2\cdot4}$ (see Appendix II). This approaches an F gait, having a markedly longer backward than forward stroke, and therefore a short body extension; the pace duration is long (column III); the angle of swing of the leg is small, possibly less than for figs. 18, 22, 19 and 20. The speed will be about 4·4 mm. per sec. for an animal of mean length 66 mm.

Thus the speeds of the animal when making these records (figs. 18, 22, 19, 20 and 21) are proportional to speeds of about 7·7, 6·0, 5·4, <6·0 and 4·4 mm. per sec. (see Appendix II), and appear to be related to each other only roughly as are the stride lengths 4·1, 3·4, 3·4–3·1, 3·1, and 2·9–2·5 mm. The relationship between speed and size has not been investigated in Peripatus, but in all the common London Myriapoda which have been examined, the speed bears a linear relationship to the length of the body, and a similar relationship probably holds for the Onychophora. Thus the actual speeds of the 50 mm. animal making the tracks may be estimated as about 5·8, 4·5, 4·1, 4·5, and 3·3 mm. per sec. in figs. 18, 22, 19, 20, and 21 respectively. Body extensions approximating to moderate were shown by the animal when making the tracks of figs. 18, 22 and 20, a shorter extension for those of fig. 19, and a considerably shorter one for those of fig. 21. A maximum extension and an E gait are not shown by figs. 18–22, but fig. 23 was made by such a gait (see pp. 536 and 539). Since the pace length cannot be determined owing to the overlapping of the sets of footprints, further analysis is not possible. The speed, however, was probably greater than in all the other records. It may be noticed that excluding fig. 23 these records show smaller angles of swing of the legs ($\theta_{2\cdot3}$–$\theta_{2\cdot7}$) than do the records obtained by cinematography ($\theta_{2\cdot4}$–$\theta_{3\cdot5}$). Figs. 18–22 may not be statistically representative, but they suggest that in the dim light under which the footprints were recorded the animal was walking in a more leisurely manner with more even stepping than occurred under the bright light used for the cinematograph records which frequently call forth maximum speeds and uneven stepping. The alternative gaits which have been shown above to be capable of giving the same stride lengths and approximately the same speeds, indicate that small differences in the angle of swing of the leg can be compensated for by alterations in the duration of the forward and backward strokes. Variations in the successive paces of the same leg are frequent under bright light (text-figs. 3–5), and their lack of interference with the speed is doubtless explained by this feature, probably combined with small local alterations in the length of the flexible body wall. This must be a serviceable latitude in the execution of a gait well suited to an irregular substratum.

The shapes of the sets of footprints in text-fig. 7 closely resemble those seen in **Pls. 16** and **17**, so that it is probable that the animal making these records had proportions much as in text-fig. 7*a*, although the exact shape of the sets in figs. 19 and 22 suggest that the last few pairs of legs were placed on the ground nearer to the middle line than in text-fig. 7*a*. The differences between the proportions shown in text-figs. 7*a* and 2*b*, and the absolute size of the animal making the tracks, in **Pls. 16** and **17**, suggest that the animal may have been a young pregnant female containing well advanced embryos in her second or third year (the rate of growth for related species is given by Manton, 1938 b).

Lastly the *footprints recorded on a white surface* (zinc oxide on black paper) while the film, analysed in text-fig. 4 was being taken will be considered. Pl. **16**, fig. 17 and text-fig. 8 show sets of footprints numbered 2–8 which were formed during the period 'p.2–8' marked above on text-fig. 4. The 2nd–8th paces of the right legs are indicated by the oblique numbered arrows. The positions of the tips of the legs during the backstroke have been plotted from the films (text-fig. 8), and if comparison be made with fig. 17 it is seen that each leg did not always leave a mark on the paper. In text-fig. 8 the heavy arrows show the positions of the middle line of the anterior

end of the body, and the dotted arrows show those of the posterior end of the body; the difference between the two indicates the lateral shift of the body as it passed these points (see also the outlines of the body at successive seconds, text-fig. 4). The small numbers mark the footprints of each leg, and sets of footprints are enclosed by dotted rings numbered 2–8.

The extreme regularity of the patterns of footprints seen in Pls. **16** and **17**, figs. 18–22 is here absent (see p. 547). Many legs were carried slowly forward missing out one or two footfalls. The footprints bounding such paces are united by curved lines, the group 'G' from the footprints of right legs 10–19 (text-fig. 8) correspond with the slow steps starting at 'G' in text-fig. 4, and similarly the group 'W' from the footprints of left legs 10–16 omitting pace 8 corresponds with the step starting at 'W' on text-fig. 4. This type of irregularity is frequent under bright illumination, but is absent from the footprints recorded under dimmer light (see also pp. 549 and 555).

The general form of most sets of footprints on text-fig. 8 is a compact unit scarcely overlapping the next set, as would be expected from a speed of 8 mm. per sec. by gait A at a moderate extension of the body (67 mm., see table I and text-fig. 2*e* interrupted line). The right sets 3 and 4 show an elongation forwards by the footprints of the posterior legs, as would be expected if the 'd' value was increased by an increase in the angle of swing of the leg (i.e. if gait A, $\theta_{2\text{-}8}$ became A, $\theta_{3\text{-}}$., table I column III), see text-fig. 2*f*, interrupted line. Probably this localized increase in the angle of swing of the leg on the right side is the cause of the bearing of the body towards the left. The widths of the 3rd and 4th sets on both sides exceeds those of sets 5–8, and this is also due to the bearing of the body towards the left, which results in the progressive lateral displacement of the footprints, see also sets 4 and 5 in fig. 22, Pl. **17**, and fig. 16, Pl. **16** where both legs of a pair (see legs 10–12) can be extended towards the same side. The alteration in the initial direction of walking on text-fig. 8, must have started after the 3rd legs had taken their 5th paces, the paired footprints of legs 1–3 in set 2–5 are almost mirror images of each other, while the footprints of the 4th pair of legs are displaced to the left in sets 4 and 5. The lengths of stride at paces 6–8 are 5·5–6·0 mm. which again corresponds with gaits A, $\theta_{2\text{-}8}$–A, $\theta_{3\text{-}2}$, (table I column I). The length of the left strides at paces 2–4 is rather less, owing to the turning of the body, a feature exaggerated in fig. 25, Pl. **17**, where the stride is relatively shorter and the turning more acute

The data here presented show that *turning* of the head end of the body from side to side may be almost continuous during locomotion in a straight line. Turning of direction of walking is accomplished by the body following a persistent turn of the head. The legs of both sides are displaced laterally in the direction of the turn, and the angle of swing of the legs on the outer side is increased without alteration of the pattern of the gait. If the turn is acute the gait changes to the F pattern, and the speed and stride length are both reduced. The posterior part of the body does not follow the path of the anterior end but becomes progressively displaced towards the side (see also p. 557).

Thus the footprints of Peripatus are very varied, each variation corresponding precisely with the employment of a particular gait. The variety of gaits in Peripatus is due to the manner of alteration of the speed. In the Myriapoda on the contrary (see Part II) changes in speed are largely effected by changes in the duration of the pace, the gait remaining the same, and the resulting footprints over a wide range of speeds may be exactly similar.

The numerical data utilized in the above account has either been based upon one animal, or has been scaled to the same approximate body size in the case of the second animal, in order to make all the data comparable for the purposes of the argument. Animals of different sizes have different speeds, lengths of stride, distances

travelled on the backstroke, values for 'd', sizes of tracks, etc., which will be proportional to their absolute sizes; but the general matters here considered concerning the pattern of the gait, the angle of swing of the leg, the duration of the pace and of the backstroke, and the pattern of the footprints, together with the effects of alterations of these factors, should be generally applicable to most if not all Onychophora.

The early evolution of terrestrial locomotion in Arthropoda.

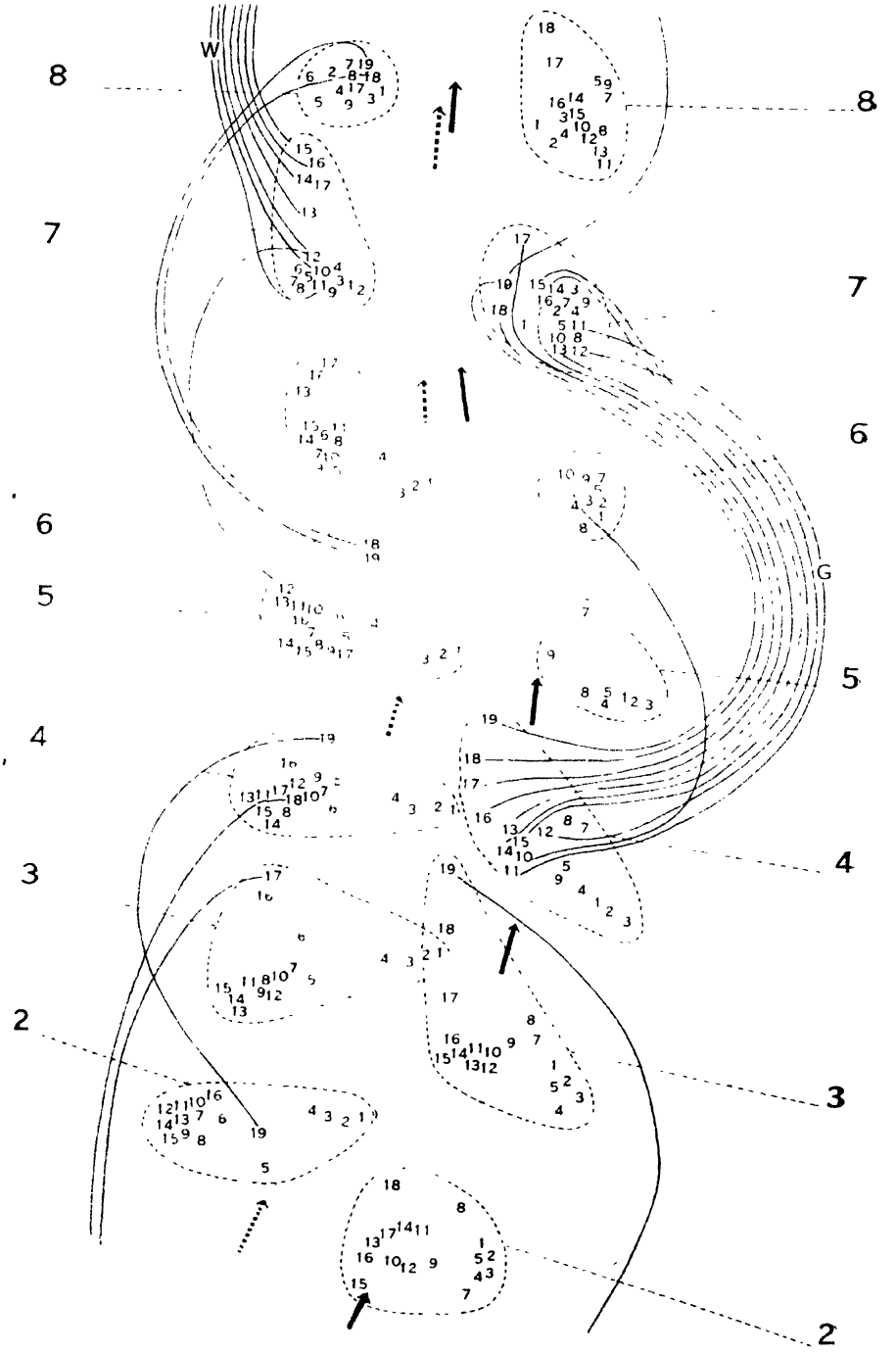
The bearing of the analysis of the locomotory movements of Peripatus upon the phylogentic origin of terrestrial locomotion in Arthropoda may now be considered. The Arthropodan type of limb is more ventrally directed than it is in the Annelida, and is capable both of supporting the body and of providing the motive force. It has been shown (p. 531) that the propulsive force for locomotion in Peripatus is provided by the extrinsic leg muscles and not by the longitudinal muscles of the body as in *Nereis* (Gray 1938). Locomotory body muscles presumably were present in the annelidan ancestor of the Arthropoda. A first change from this condition must have been a reduction in the propulsive force provided by the longitudinal body muscles and an increase in that supplied by the extrinsic muscles of the limbs, and this may have occurred as the parapodia became more ventrally directed. When the undulations of the body ceased to be locomotory, the limbs of a pair would become free to move in alternate phase as before, or to move synchronously (the latter being incompatible with locomotory undulations of the body). If the paired limbs continued to move in alternate phase lateral flexures of the body might persist, but if the limbs were predominantly in phase the body would be straight. It has been shown above (pp. 547 and 553) that the employment of a variety of gaits by Peripatus is associated with the manner of alteration of the speed of progression, and that this also results in a variety of phase relationships between legs of a pair. Little support is therefore given for the view that an Arthropod with paired limbs in phase with each other is necessarily more primitive in this respect than one showing paired limbs in alternate phase, although the execution of a 'bottom gear' gait, either alone, or predominantly, may have been a first stage in the evolution of terrestrial locomotion In the higher Arthropoda the gaits performed by each animal are restricted, and the phase difference between legs of a pair becomes correspondingly fixed (see Part II).

It has been shown that different degrees of longitudinal extension of the body and limbs in Peripatus are associated with the several gaits (pp. 530, 533, 551, and text-fig. 6). It is not known why different gaits should be more easily carried out at different extensions of a segment (work is in progress on this subject), but the mechanism effecting these changes in shape must reside in the musculature and the haemocoel. Lankester (1904) pointed out that all existing Arthropoda have an ostiate heart and have undergone phloebedesis, or the dilatation of the peripheral vascular system at the expense of the coelome. Phlebodesis presumably preceded the stiffening of the integument as the Onychophora at the present day have not advanced beyond this stage.

Changes in speed of progression in Peripatus are carried out largely by an alteration in the gait, there being little change in the duration of each pace. In the Myriapoda on the contrary, changes in speed are mainly effected by alterations in the pace duration, the gait remaining the same. The latter condition is presumably associated with the presence of an exoskeleton and the former with a soft body wall.

Text-fig. 8.

The footprints shown in fig. 17, Pl. 16, are here plotted from the cinematograph film taken at the same time (see text-fig. 4). For general description see p. 561. The small numbers represent the middle of the footprint formed by the sub-terminal pad of spines on the leg. The dotted lines extending from the dotted rings surrounding each set of footprints are roughly set at right angles to the direction of movement of the anterior part of the body when it was passing this point. These lines, together with the heavy and dotted arrows representing the middle line of the anterior and posterior ends of the body, indicate the bearing of the body first to the left and then to the right. The groups of right legs which omit footfalls 5 and 6 'G' and left legs which omit footfalls 8 'W' are also shown in text-fig. 4 starting at 'W' and 'G'.



TEXT-FIG. 8.

[For legend see p. 562.

As the legs of a soft bodied ancestral Arthropod became of greater locomotory significance, varying speeds of progression would also be desirable. Since a change in speed is most easily carried out by a change in the gait in a soft bodied animal such as Peripatus, alterations in the extension of the segments would be expected to appear in association with an ability to change the speed.

Lankester and Cannon have appreciated a functional advantage consequent upon phleboedesis which may have operated before the integument hardened. 'On contraction of any part of the body any other part of the body can be distended or made rigid by distension' (Cannon, personal communication). Such alterations in shape may be more easily effected by a haemocoel than by a coelome, as coelomic fluid does not circulate and can only move freely where mesenteries and septa are broken down, and the coelome is usually in communication with the exterior. Annelids do show alterations in shape caused by muscles displacing coelomic fluid, but these changes are more local than those in Peripatus, and presumably also more local than those in an ancestral soft bodied arthropod that became capable of changing its speed of walking by changing the gait. Thus a functional suggestion is presented for both the origin of and the need for the arthropodan haemocoel, which it is hoped may be furthered by future work.

The fossil record gives us little direct evidence concerning the origin of terrestrial Arthropoda. Tiegs (1948) has surveyed the evidence in favour of the Insecta and Myriapoda having a common origin from some terrestrial Peripatus-like ancestor which was distinct from the aquatic Trilobite–Crustacean–Arachnid branch with more complex legs. The fossil *Aysheaia* Walcott (Hutchinson 1930) from the middle Cambrian, whether it be closer to the Annelida or to the Arthropoda, is strikingly like the modern Onychophora in body and limbs, excepting the more elaborate antenna and the more primitive condition of the head. It was certainly marine, and, since its limbs so closely resemble those of Peripatus, it is not unreasonable to consider that they were moved in a comparable manner, and if so, the haemocoel may have already started its development. Thus the acquisition of propulsive extrinsic limb muscles and a lack of an undulatory body may have preceded emergence from the water. The Onychophora like the Amphibia clearly developed many structures essential to land life before they emerged from the water, and their ancestors had probably evolved the essentials for terrestrial locomotion long before they left the sea. It is significant that the amphibious Crustacean *Ligia* (see a subsequent Part) employs the same gait in the sea and on land, the pace duration being shorter and the speed consequently greater in air. The Onychophoran marine ancestor may have penetrated into fresh water before becoming terrestrial, or it may have walked directly up the beach into damp surroundings just above high water level, such as can be found in some estuaries today where woods lie immediately above a beach protected from rough weather. Presumably the integument of the earliest land Onychophora was wetable, and an ability to retain the salt content of the body, and to eliminate water absorbed osmotically, must have been two of the many essential requirements. The secretion of hypotonic urine by *Peripatopsis* may be a survival from a time such as this 'when the retention of salt was an important factor in the control of the internal medium' (Picken 1936). The locomotory movements of the Onychophora have probably remained fundamentally the same during these changes of environment. The further evolution of the locomotory mechanisms and of the attendant body forms in the Arthropoda provided with a stiff integument will be considered in Part II.

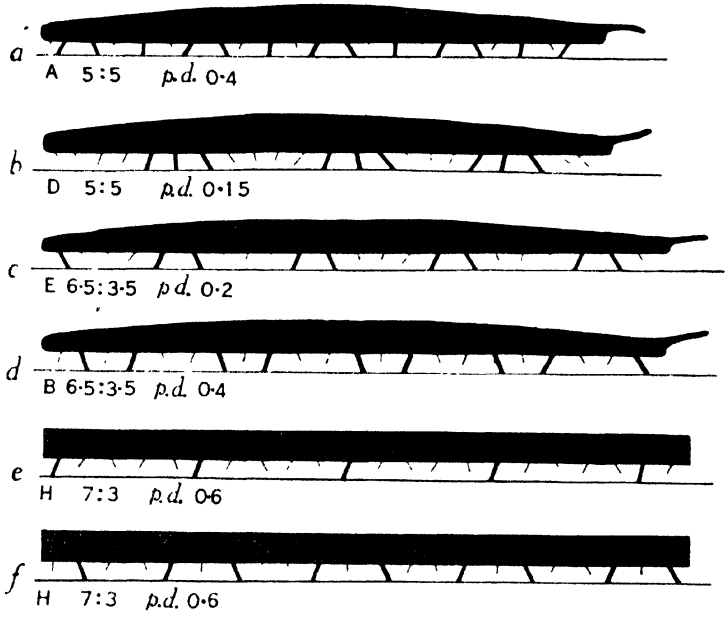
ACKNOWLEDGMENTS.

My thanks are due to Professor J. Gray and to Dr H. W. Lissmann for taking the cinematograph films, and to Dr Lissmann for preparing paper coated with zinc oxide. The photographs in Pl. 15 were taken by Mr D. P. Wilson. To Dr J. P. Harding I am indebted for the manufacture and manipulation of the photographic apparatus used for analysing the films, and for many other services.

APPENDIX I.

ON THE DISPOSITION OF THE LEGS WHICH ARE IN CONTACT WITH THE GROUND.

In order to ascertain the positions which a series of legs would assume during a regular execution of any one gait, the movements of a series of limbs at a specified phase difference and relative duration of forward and backward strokes must be plotted as in text-fig. 1, and the series extended until the requisite number of legs is shown, or until a repeat of the pattern appears. Vertical lines across this series will then indicate the disposition of the legs at any one moment (see the vertical rows of dots in text-figs. 3–5).



TEXT-FIG. 9.

Silhouettes of an animal of the same volume as the *Peripatopsis* shown in text-fig. 6 but walking at different gaits. The extensions of the body are either those which have been observed, or in the case of theoretical gaits, are those calculated for the gait. The positions of the legs are those calculated(see Appendix 1) for a regular performance of each gait.

Fig. 9*a*.—*Peripatopsis* progressing by gait A with relative durations of forward and backstrokes as (5 : 5) and a phase difference between successive legs of 0·4 (see fig. 10, Pl. **15**)

Fig. 9*b*.—*Peripatopsis* progressing by gait D with relative durations of forward and backstrokes as (5 : 5) and a phase difference of 0·15.

Fig. 9*c*.—*Peripatopsis* progressing by gait E with relative durations of forward and backward strokes as (6·5 : 3·5) and a phase difference of 0·2 (see fig. 12, Pl. **15**).

Fig. 9*d*.—The calculated appearance of the same *Peripatopsis* if it progressed by gait B with relative durations of forward and backward strokes as (6·5 : 3·5) and a phase difference of 0·4.

Fig. 9*e* and *f*.—The calculated appearance of the same number of segments of an animal constructed as is Peripatus, at two different moments, in the execution of gait H with relative durations of forward and backward strokes as (7 : 3) and a phase difference of 0·6.

For each pattern of gait the average number of legs in contact with the ground at one moment is proportional to the relative duration of the backstroke (see p. 534). This number represents an average of all moments during the gait, but may in fact never be realized at every or even at any one moment during an exactly regular performance of a particular gait. For example gait A (5 : 5), in which half of the pace is occupied by the backstroke, shows at a phase difference of 0·4 (text-fig. 9*a*) a total of about 9* propulsive and 13* recovering legs out of a total of 22, or vice versa, and the average of half of the legs in contact with the ground at one moment is never realized. The same type of gait (5 : 5) at a phase difference of 0·45 (text-fig. 6*b*) shows 12 propulsive legs and not the average of 11. Similarly, the E gait (6·5 : 3·5) at a phase difference of 0·2 (text-fig. 9*c*) shows 9 propulsive legs and not a number closer to the average of 7·7. Thus a divergence at any one moment from an average number of propulsive legs expected for any particular gait is not due to irregular stepping. It is inevitable if the execution of the gait is regular, and is compensated for by an equal and opposite divergence at another moment.

Certain gaits show the same general disposition of legs at all moments, and other gaits can show very different dispositions. For example a B gait (6·5 : 3·5) at a phase difference of 0·4 always appears as in text-fig. 9*d*. The A gait referred to above at a phase difference of 0·4 shows two alternative dispositions, either as in text-fig. 9*a*, or with about 9* propulsive and 13* recovering legs. The calculated appearance of a similar number of segments and legs at gait H (7 : 3) and a phase difference of 0·6 is shown at two different moments in text-fig. 9*e* and *f*. This gait cannot be executed by Peripatus but may be performed by some Myriapoda. The two moments are of strikingly unlike appearance.

Further, certain unlike gaits may show an exactly similar disposition of the legs at particular moments, although the body extension may be different. For example gait A (5 : 5) at a phase difference of 0·4 (text-fig. 9*a*) for one moment in every pace shows a disposition of its legs exactly resembling that of the B gait (6·5 : 3·5) at a phase difference of 0·4 shown in text-fig. 9*d*.

Thus in making any deductions concerning gaits from still photographs it must be remembered (1) that the theoretical average number of propulsive legs for a gait may never be achieved, (2) that the same gait may show markedly unlike disposition of legs at different moments, and (3) that rarely different gaits may show exactly the same disposition of legs upon the ground. Therefore a diagnosis of a gait from a still photograph must be carried out by a consideration of factors additional to the disposition of the legs. In the above examples particular attention has been paid to the positions of the propulsive legs. Where these may be relatively few, as in certain fast Myriapodan gaits, the detailed disposition of the legs off the ground may be useful in diagnosing a gait from a photograph.

APPENDIX II.

Analysis of tracks

A method is here given for ascertaining the gaits which could give the tracks shown in figs. 18–22, Pls. **16** and **17**, by deduction from the data presented in a fuller table I (p. 540), by the length of the stride, and by the value of '*d*' given by reference to text-fig. 7 (see p. 557). The stride lengths of the 50 mm. animal must be scaled to correspond with those of an animal of mean length 66 mm., and for figs. 18, 22, 20, 19 and 21, will read 5·5, 4·6, 4·6–4·1, 4·1 and 3·8–3·5 mm. respectively. The speeds for each gait shown by the table are for an animal of mean length 66 mm., and will be proportional to those of the 50 mm. animal which made the tracks. The relationship between speed and the length of the body is probably linear, see p. 560. Where two theoretically extreme gaits are shown to be capable of giving the same tracks both are usually impracticable, and the practicable gait which actually formed each track

* The exact number depends on the repeat of the metachronal wave.

is intermediate between the extremes. The practicability of the gaits is considered on p. 559.

Fig. 18. If a pace length of 5·5 mm. is sought for in column I table I it is found that gait A, $\theta_{2\cdot7}$ possesses this pace length, and also a 'd' of 3·3 mm. and a speed of 7·7 mm. per sec. This value of 'd' is 0·2 mm. lower than the value 3·5 mm. indicated by shape of the sets of footprints (text-fig. 7*b*). Gaits with similar durations of forward and backward strokes (such as an A and a D gait) and also the same speeds and stride lengths, will have values of 'd' which correspond with the respective phase differences between their successive legs (p. 542). Thus a gait resembling A, $\theta_{2\cdot7}$, but possessing a higher value of 'd', must have a smaller phase difference between successive legs than the 0·4 shown by gait A, and approach that of gait D with a phase difference of 0·15. The difference between the phase relationships of an A and a D, or of a C and an F gait is 0·4–0·15 = 0·25, and the difference between the 'd' values of gait A, $\theta_{2\cdot7}$ and D, $\theta_{2\cdot7}$ is about 1·44 mm. Thus a 1·44 mm. difference in 'd' corresponds with a difference in phase relationship of 0·25, and a 0·2 mm. difference must therefore correspond with a difference in phase relationship of about 0·035. Thus a gait which could give the tracks has a phase difference of 0·4–0·035 = 0·36, and can be briefly expressed as (A, 0·36) $\theta_{2\cdot7}$, the figure within the bracket indicating the phase difference between successive legs.

Fig. 22. The procedure is as above, but two alternative extensions of the body and values of 'd' must be considered, 3·35 mm. for a moderate extension, and 2·9 mm. for a short extension of the body (p. 559 and text-fig. 7*c* and *a*). A pace length of 4·6 mm. is given by gait A, $\theta_{2\cdot3}$ (moderate body extension) and also by gait F, $\theta_{3\cdot3}$ (short body extension). An A gait usually shows a short pace duration (column I) and an F gait a longer one (columns II and III) or even longer. Gait A, $\theta_{2\cdot3}$ in column I table I has a 'd' of about 2·8 mm. and a speed of about 6·5 mm. per sec.; this 'd' value is too low by 0·55 mm., so the required gait will have a calculated phase difference of about 0·28, which is about half way between an A and a D gait. Gait F, $\theta_{3\cdot3}$ in column III has a 'd' of about 4·0 mm. and a speed of about 5·4 mm. per sec.; this 'd' value is too high by 1·1 mm., so the required gait here has a phase difference of 0·36, which is practically a C gait. These two gaits (A–D, 0·28)$\theta_{2\cdot3}$ and (C–F, 0·36)$\theta_{3\cdot3}$ and all intermediate ones could give tracks as in fig. 22 at speeds ranging from 6·5–5·4 mm. per sec. for an animal of mean length 66 mm.

For figs. 19 and 20 the procedure is as for fig. 22, two alternative values of 'd' being taken for a short and a moderate extension of the body, and from the table a pair of theoretical gaits giving the same stride length can be deduced for each, between which all intermediate gaits give similar tracks.

For fig. 21 the procedure is as for fig. 18, one value of 'd' at a short body extension being used.

SUMMARY.

1. The head and antennae carry out rhythmical movements during walking, and the antennal sensory hairs sometimes touch the ground.

2. Walking is effected by the propulsive force of the extrinsic limb musculature, the rigidity and length of the leg being controlled by the intrinsic muscles. The longitudinal body muscles, which provide the main propulsive force in many annelids, are concerned in the Onychophora with maintaining a fairly rigid body wall for the operation of the extrinsic limb muscles. It is suggested that a transference of the origin of the propulsive force from the body to the limb musculature may have been an important step in the evolution of supporting limbs and of terrestrial locomotion in the Arthropoda.

3. A variety of gaits occur in which the duration of the pace, the relative durations of the forward and backward strokes, the angle of swing of the legs, and the phase difference between successive legs, vary independently. The resultant speeds and lengths of stride depend on these factors and on the absolute size of the animal.

4. Changes in the length of the body of up to $\pm 12\%$, and alterations in the extension of the legs, accompany changes in the gait. The longer extensions of the body and legs accompany gaits with relatively short durations of the backstroke, and give the faster speeds. The length of the legs also changes during each backstroke.

5. The relationships are given between the gait, the speed, and the number of points of contact with the ground. Fewest contacts are usually, but not always, associated with the faster speeds. Changes of speed are mainly effected by changes of the pattern of the gait, the pace duration being little altered.

6. The form of the tracks depends on (1) the stride length, (2) the distance travelled during the time interval between the putting down of one leg and of the next behind it, and (3) on the dimensions of the body and degree of longitudinal extension. The patterns differ greatly for different gaits and extensions of the same animal.

7. The theoretical gaits which might be performed by an animal are compared with those which actually occur. Three gaits are predominantly used; one for starting to walk and gaining speed, another for moderate or fast walking, and a third for easy walking when momentum has already been achieved. The relative durations of the forward and backward strokes in these gaits respectively are as 3·7 : 6·3, 5 : 5 and 6·3 : 3·7 (approximately), and the phase differences between successive legs in the three gaits are 0·16, 0·4 and 0·16–0·2 (approximately).

8. The paired legs step approximately in phase with each other during the 'bottom gear' (3·7 : 6·3) gait, and approximately in alternate phase during the 'top gear' (7·5 : 3·7) gait. In the 'middle gear' (5 : 5) gait the phase relationship is variable and fluctuating. The longitudinal coordination between legs of one side of the body appears to be stronger than the coordination between legs of a pair.

9. The method of turning is described.

10. The evolution of the Onychophoran locomotory mechanism from that of an Annelidan ancestor is discussed.

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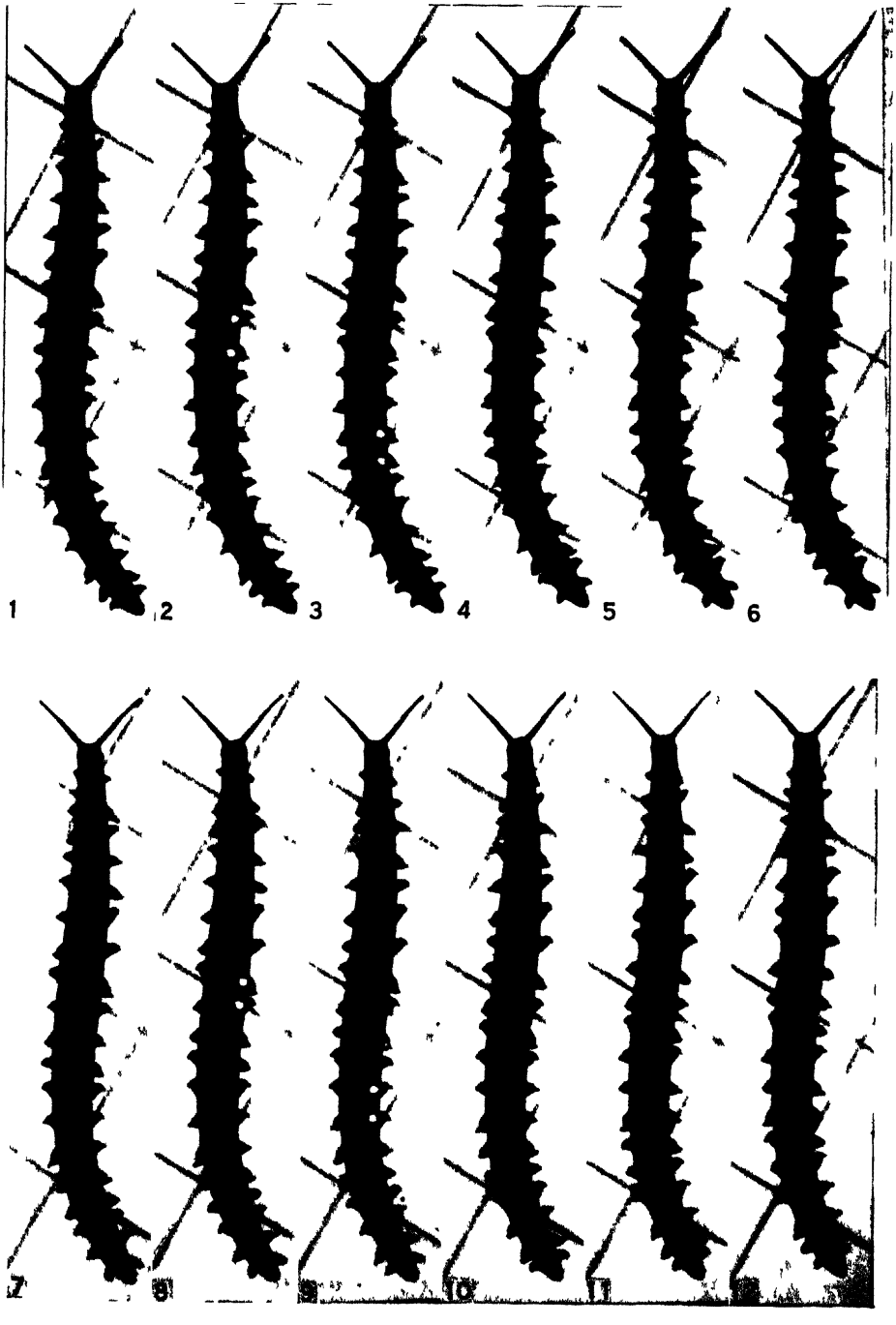
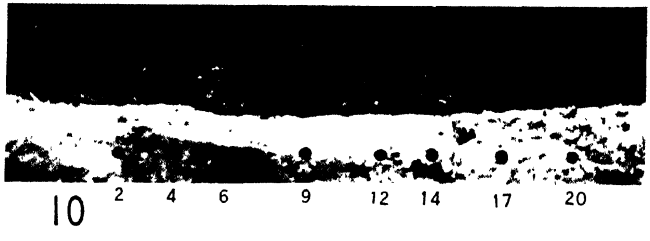


Locomotion of *Peripatopsis*



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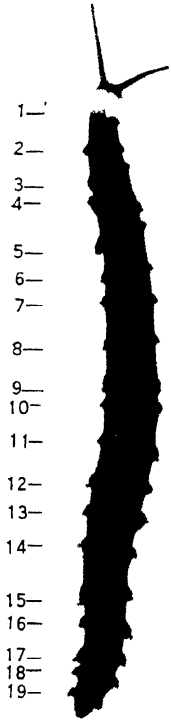

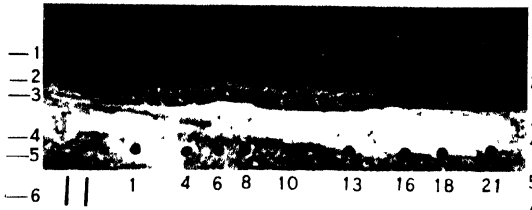

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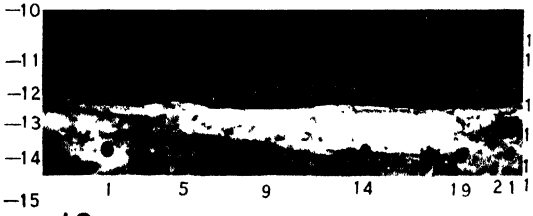

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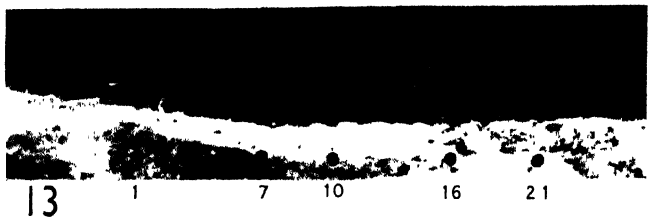

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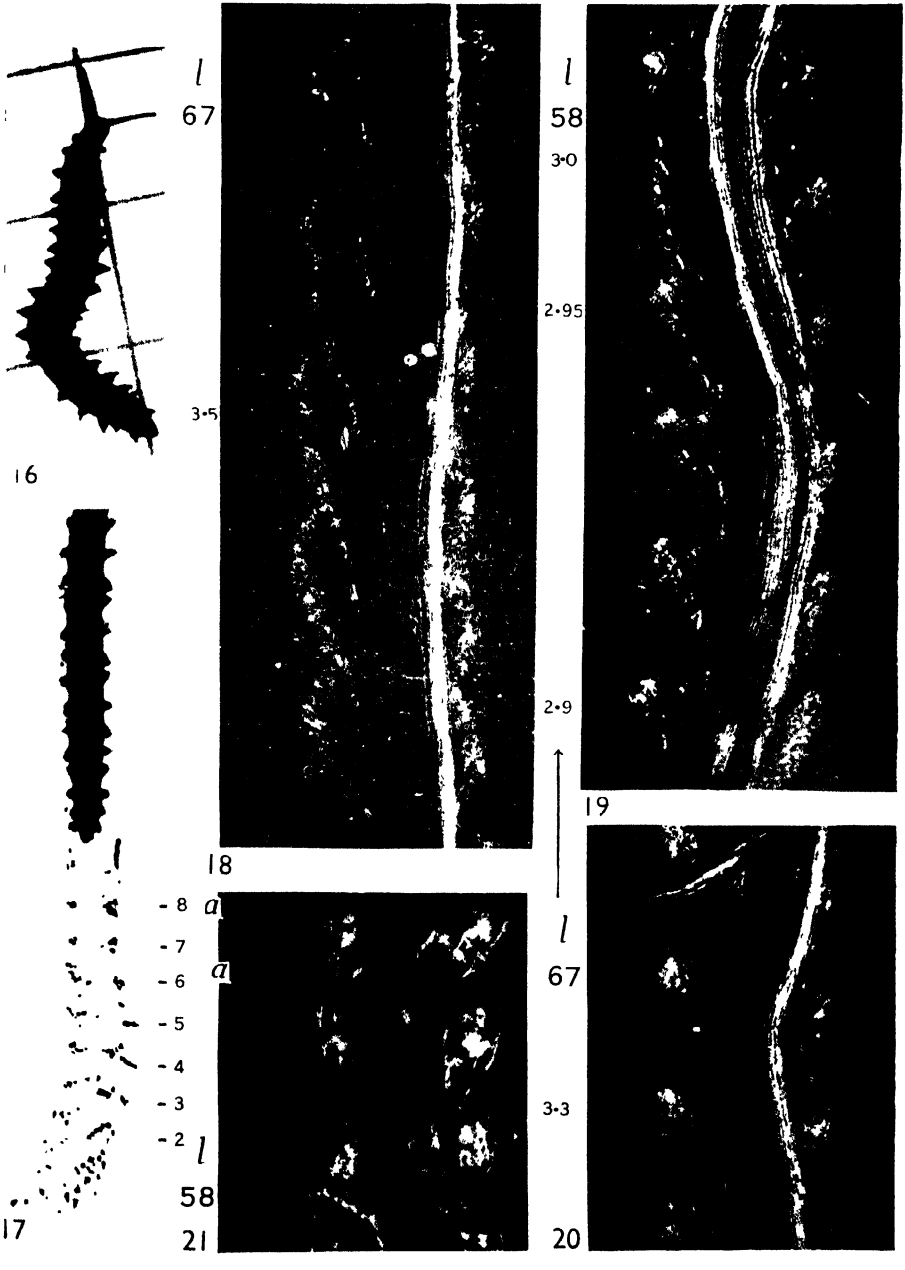
Locomotion of *Peripatopsis*.



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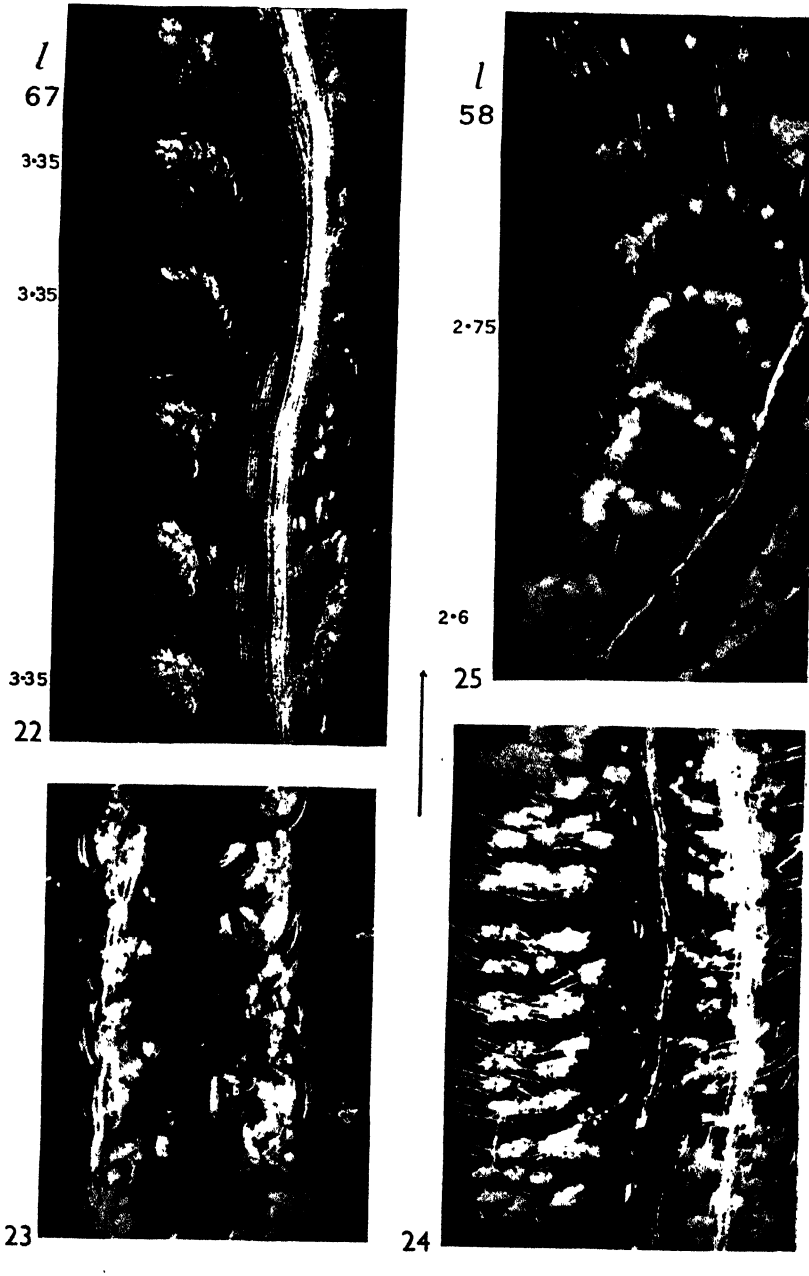

Locomotion of *Peripatopsis*

EXPLANATION OF THE PLATES.

PLATE 14.

Successive photographs of *P. sedgwicki* from the film analysed in text-fig. 3, over the period marked 'p'. The time interval between the photographs is 1/14th sec.; the background is divided into 2 cms. squares. A complete step is shown by about 10 frames, for example the right second leg is put on the ground in frame 2; it is raised and starting the forward swing, during which the body carries the leg forwards, in frame 8, and it is put down on the ground again in frame 11. The sixth right leg is not used. For explanation of the white dots see p. 531, the dots have been marked on the prints. 1·3

PLATE 15

Figs. 10–13 show lateral views of two different specimens of *Peripatopsis moseleyi* when walking. The body is raised off the substratum, but in the animal shown in figs. 10 and 13 the legs are more ventrally directed than in the animal shown in figs. 11 and 12. The legs at or near the end of the backstroke are marked; where the phase difference between successive legs is small a larger number of legs participate in each metachronal wave of limb movements than where the phase difference is large.

Fig. 10 shows approximately 7 cycles of leg movements, and the short legs 21 and 22 are carried clear of the ground. The gait is of the (5 : 5) pattern at a phase difference of 0·4 (see text-fig. 9*a*). The speed is probably moderate, and faster than in fig. 13.

Fig. 11 shows approximately 8 cycles of leg movements, with approximately every other leg on the ground. The gait is of the (5 : 5) pattern at a phase difference of 0·45 (see text-fig. 6*b*). The speed is probably moderate or fast.

Fig. 12 shows approximately 5 cycles of leg movements, and up to five consecutive legs in each metachronal wave, three of these being clear of the ground. The extension of the body is 10% greater than in fig. 11. The gait is of the (6·5 : 3·5) pattern at a phase difference of 0·2 (see text-fig. 9*c*). The speed is probably faster than in fig. 11.

Fig. 13 shows approximately 4 cycles of leg movements, and up to six consecutive legs in each metachronal wave, many of which appear to be in contact with the ground. The gait is of the (3·7 : 6·3) pattern at a phase difference of 0·16 (see text-fig. 6*a*). The extension of the body is 17% less than in fig. 10, and the angle of swing of the legs is than in fig. 10. The speed was probably slow.

Figs. 14, 15 show the same specimen of *P. sedgwicki* walking at two different extensions of the body, and showing different positions and extensions of the antennae. The length in fig. 15 is 9% less than in fig. 14. This same animal is shown in pl. XIII, fig. 2 (Manton 1938*a*) at a 11% lesser extension of the body than seen in fig. 15.

PLATE 16

Fig. 16. Photograph of the *P. sedgwicki* seen in Pl. 14 and in fig. 17 in an irregular position showing varying leg postures. The conspicuous bend to the left in the middle of the body is being eliminated, and legs 10–12 are stretched towards the left from both sides of the body, and leg 9 on both sides is stretched to the right at the beginning of a step. 1.

Fig. 17. Tracks left by *P. sedgwicki* walking over black paper coated with zinc oxide powder at the same time as the record shown in text-fig. 4 was made. The numbers 2–8 mark the sets of footprints which have been analysed from the film and shown in text-fig. 8. The elongated black mark between the animal and the 8th sets of footprints was caused by the 6th right leg being dragged along the substratum. 1

Figs. 18–25 show enlarged photographs of the tracks made by another *P. sedgwicki* about 50 mm. in length, when walking over smoked paper. The tracks are composed of paired sets of footprints, each set comprising the footprints of the legs of one side of the body. The 1st set is at the bottom, and the 2nd–6th sets lie progressively towards the top of each record. On the right a leg has been dragged across the substratum. In figs. 18–20 the legs of a pair are a little out of phase so that the sets of footprints on each side are not opposite one another. Claws were used only in figs. 24 and 25. The numbers on the left of some of the sets of footprints give the values of 'd' corresponding with the calculated patterns for an animal of similar proportions (text-fig. 7a) but showing either an approximately moderate extension of the body of 67 mm. '/67' or a shorter extension of approximately 58 mm. '/58'. For further description see pp. 556–560 and Appendix II.

Fig. 18. The sets overlap forwards, the stride length is about 4·2 mm., and the width of the track about 5·05 mm. The estimated extension of the body was moderate, and the speed probably faster than for figs. 19–22, see p. 558. 5.

Fig. 19. The first two sets are separate, and the subsequent sets progressively elongate with increasing values of 'd' till they touch each other at paces 4–6, the stride length of leg 1 is 3·1 mm. and those of the middle and posterior legs increase slightly, and the width of the track is about 4·9 mm. The estimated extension of the body and also the speed was less than in figs. 18, 21 and 22 and greater than in fig. 21, see pp. 559 and 560. 5.

FIG. 20. All sets show the minimum size and approximate to a large dot, the stride length is 3·4–3·1 mm., and the width of the track is about 4·7 mm. The estimated extension of the body was shorter than in fig. 18 but longer than for figs. 19 and 21; and the probable speed was slightly less than in fig. 22, considerably less than in fig. 18, and greater than in figs. 19 and 21, see p. 559. > 5.

FIG. 21. All sets are compact, but less so than in fig. 20; the stride length is 2·9–2·5 mm., and the width of the track about 4·4 mm. The estimated extension of the body and also the speed was less than in figs. 18–20 and 22. Two series of marks 'a' have been left by sensory hairs of the left antenna, see p. 560. 5.

PLATE 17.

FIG. 22. The sets are separate, and set 1 has the same general form as set 1 on fig. 19, the lateral spread of sets 4–5 is due to a slight bearing to the left. The pace length is about 3·4 mm., and the width of the track is about 5·1 mm. The estimated extension of the body was moderate, and the speed probably greater than in figs. 19–21 but less than in fig. 18, see p. 559. > 5.

FIG. 23. The sets are here long and overlap greatly so that they are no longer recognizable, being of the type shown in text-fig. 2*h*; the width of the track is about 5·1 mm. The estimated speed is greater than in figs. 18–22, see pp. 557 and 560. < 5.

FIG. 24. Tracks left by an animal which was shuffling about slowly and using its claws. 5.

FIG. 25. The left sets are shown at a turn towards the left: the change of direction is greater in the upper part of the record than in the lower part. The sets overlap backwards and not forwards as in fig. 18, and the superimposed parts can be recognized by reference to text-fig. 7; the lateral spread of each set is progressively increased. The stride length is about 2·2 mm. The estimated speed was slower than in figs. 18–23, see pp. 557 and 561. 5

Mexican and Central American Garter Snakes (*Thamnophis*) in the British Museum (Natural History).

By Hobart M. Smith, C. William Nixon, and Philip W. Smith. (Communicated by H. W. Parker, M.A., F.L.S.)

[Read 25 November 1948]

Summaries of neotropical garter snakes published since 1900 (Ruthven, 1908; Fitch, 1940. Smith, 1942. Smith and Taylor, 1945) have been based almost exclusively upon specimens in American museums. The large collections of European museums, particularly of the British Museum (Natural History), were neglected because of the mechanical difficulties of examining them.

Early in 1947, Mr. Roger Conant, more diligent than most of his colleagues and predecessors, arranged through the good will and courtesy of Mr. H. W. Parker of the British Museum, to examine all neotropical specimens of the Boulengerian (1893) genus *Tropidonotus*, chiefly for the purpose of examining the members of the group currently recognized as the genus *Natrix*. Included also, however, in Boulenger's *Tropidonotus* is the genus *Thamnophis* of current nomenclature. Very generously Mr. Conant arranged to share the fruits of his industry by making the specimens of the latter genus available to us for study. We are deeply grateful both to Mr. Conant and to Mr. Parker for this opportunity.

Among the specimens now assembled in the genus *Thamnophis* are 79 from Mexico and Central America the British Museum possessed at the time Boulenger's catalogue (1893) was published; it now possesses 108. Then, 9 species and subspecies were recognized; we list 17—somewhat better than half the 31 currently recognized in Mexico and Central America. The 79 specimens available to Boulenger actually represented 14 species and subspecies, as now understood.

The present summary provides at least brief notes on all except 6 (cotypes of *T. s. godmani*) of the 108 specimens in the British Museum, a description of two new races (one of which is not represented by specimens in the British Museum but whose validity was indicated by their specimens of a named race previously confounded with the unnamed subspecies), and certain novel distributional and variational data.

Thamnophis chrysocephalus (Cope).

Seven specimens are from three localities—five from Omilteme, 8,000 ft., Guerrero (1893.1.9.5–7, collected by H. H. Smith and presented by Godman; 1894.11.14.17, from Godman; and 1906.6.1.249, collected by Gadow); one from Amula, 8,000 ft., Guerrero (1893.1.9.8, collected by Smith, presented by Godman); and one from Jalapa, Veracruz (1881.10.31.58, collected by Hoege).

Boulenger (1893, 203) listed only four specimens of *T. chrysocephalus*, these are apparently Nos. 5, 6, 7 and 8 of the preceding list. Specimens which were acquired later were Nos. 249 and 17 of the preceding list, while Boulenger apparently omitted the specimen from Jalapa, No. 58, even though the collection date was 1881.

These specimens are noteworthy in two respects: (1) they provide evidence that both colour phases (*typicus* and *eburatus*) occur throughout the range of the species, thus indicating still further that the latter phase is not taxonomically distinct; and (2) they prove the occasional occurrence of a short mid-dorsal stripe anteriorly.

Two specimens (No. 2 from Omilteme and No. 58 from Jalapa) are of the peculiar dark (*eburatus*) phase, having a black belly and dorsum and a very prominent, wavy, whitish lateral line. This phase has not been recorded heretofore from Guerrero.

In two specimens (No. 249 from Omilteme, and No. 58 from Jalapa) a mid-dorsal light stripe is clearly evident a short distance on the neck. Both are juveniles, and in one the short mid-dorsal stripe appears possibly to have resulted from fading.

No evidence has been discerned of taxonomically significant geographic variations, although three faunistically distinctive areas are inhabited (the Veracruz, Oaxaca and Guerrero areas). It may be of interest, however, that two post-oculars have been recorded only from Oaxaca, and, with one exception, 7 supra-labials only from Guerrero.

This species, often confused with *T. scalaris*, can easily be distinguished by its larger eye, and almost always by the absence of a mid-dorsal stripe and presence of 8 instead of 7 supra-labials.

THAMNOPHIS EQUES EQUES (Reuss).

Fourteen specimens are from the following localities. *Durango:* Ciudad (Nos. 1882.11.15.21, 26; collected by A. Forrer; *Zacatecas:* Mezquital del Oro, 4,500 ft (No. 1892.2.8.54; collected by A. C. Buller); Zacatecas (No. 1885.6.20.1; presented by J. M. Cameron); *Jalisco:* North of Río Santiago (Nos. 1892.1.9.9–10, presented by F. D. Godman); La Venta, Guadalajara, 5,132 ft. (No. 1892.2.8.53, collected by A. C. Buller); *Guerrero:* Chilpancingo (No. 1893.1.9.11, collected by H. H. Smith); Amula, 8,000 ft. (Nos. 1893.1.9.13–15, collected by H. H. Smith); Omilteme (No. 1894.3.1.10, collected by F. D. Godman); Xucumanatlán (No. 1893.1.9.12, collected by H. H. Smith, presented by F. D. Godman); *Veracruz:* Jalapa (No. 1881.10.31.59, collected by Hoege). The race has been previously recorded in all these states, but a number of areas of considerable interest are represented.

Only one specimen in this series, from Omilteme, was not available to Boulenger (1893 : 209). In turn, Boulenger lists ten specimens not included here: seven from Ciudad Durango, one from 'Rio Chisoy,' another from Dueñas, Guatemala, and a final one from 'Guatemala.' All are still in the museum collection. The latter three are here regarded as representatives of two subspecies (one of them new) of the species *T. sumichrasti*. The seven from Durango all belong to the species *T. errans*.

The two specimens from 'North of Río Santiago' are peculiar in ventral scale counts. The male possesses fewer ventrals (155) than any recorded *T. e. cyrtopsis* (163 minimum) while the female possesses more ventrals (174) than any recorded *T. e. eques* (maximum 164). Were locality data not available we would regard the female as *T. e. cyrtopsis* and the male as *T. e. eques*, with which they well agree. In fact, there is grave doubt in our minds that both were actually collected in Jalisco, although one (the male) may well have been. It is true that previous information indicated western Jalisco and eastern Nayarit as probable areas of intergradation of these two races, and the present specimens lend credence to the idea. It is unfortunate the locality is so uncertain that only northern Jalisco is assured. It may be supposed, however, that the specimens were secured in the extreme western (and of course northern) part of the state, since presumably typical *T. e. eques* is known from the eastern (Belén [Belém de Refugio according to some atlases]) and central (20 km. south of Guadalajara) portions.

The Santiago specimens lend some credibility to the allocation of two specimens (by Smith, 1942 : 108) from northern Nayarit (Santa Teresa) to *T. e. cyrtopsis*, despite the extreme southern position of this locality, and the close approximation to Guanacevi, Durango, where typical *T. e. eques* is recorded. Presumably, if correctly understood, *T. e. cyrtopsis* extends southward only west of the Sierra Occidental in this area, while east of the divide *T. e. eques* occurs. Northward, of course, *T. e. cyrtopsis* occurs on both sides of the divide. Until a larger series is available from the vicinity of Santa Teresa or elsewhere to the north or south on the Pacific slopes of the Sierra Occidental, any allocation of the small series now available from there should be considered tentative.

The Guadalajara specimen, consisting of head and neck only, appears to be typical of the race. It represents a large adult.

The two from Ciudad, Durango, appear typical of *T. e. eques* and verify previous reference of specimens from central and southern Durango to this race.

The two from Zacatecas are typical *T. e. eques*. The one from Mezquital del Oro is from the extreme southern part of the state, virtually straight north of Guadalajara and 'north of Rio Santiago'. It, therefore, indicates that at least one of the specimens (see above) which actually bear the latter locality data was indeed taken farther west (and perhaps north) than the Guadalajara area.

The fine series from Guerrero exhibits no noteworthy variation from the normal for *T. e. eques*, save the occurrence in one female of the ventral count of 144, one less than the minimum previously recorded. Four post-oculars occur more frequently in Guerrero specimens than in others, but the frequency is not sufficiently great to serve as a basis for subspecific recognition.

The specimen from Jalapa is typical. It is probable that it came from the mountains west of town.

THAMNOPHIS EQUES CYRTOPSIS (Kennicott).

Two specimens (Nos. 1911.12.12.20–21, collected by Neilly and presented by Hans Gadow) are from Ioquiro (probably Yoquivo), Sierra Tarahumare, Chihuahua. Neither of these specimens was available to Boulenger (1893). They possess the high ventral counts typical of this race, but as characteristic of southern specimens, have the narrow mid-dorsal stripe universal in *T. e. eques*. It may well be that the populations possessing this combination, since they occupy a considerable range and are more or less uniform, deserve nomenclatorial recognition despite their obvious hybrid origin. No name for it is available at the present time.

The two specimens (No. 20 a male and No. 21 a female) mentioned above exhibit respectively the following variations: scale rows, 19–19–17, 19–19–17; ventrals, 178, 176; caudals, 86, 72 ; supra-labials, 8-8, 8-8; infra-labials, 10–10, 10–10; pre-oculars, 1-1, 1-1; post-oculars, 3-3, 3-3; total length, 355 mm., 342 mm. tail length, 84 m., 77 mm.; ratio of tail to total length, 0·237, 0·225

THAMNOPHIS ERRANS Smith.

Among the rarities of the collection is a fine series of eight specimens of this species, from Ciudad, Durango (Nos. 1882.11.15.22–25, 27–29, collected by A. Forrer), and Ioquiro (probably Yoquivo), Sierra Tarahumare, Chihuahua (No. 1911.12.12.20). Boulenger (1893 : 209) lists the seven specimens from Ciudad, Durango under *T. ordinatus eques*. The eighth specimen, from Chihuahua, was collected in 1911, and, therefore, was not included in Boulenger's work. Only six other specimens have ever been recorded of the species, although both states were represented by them. The present series is of value in establishing more accurately the variation of the species.

The mid-dorsal light stripe is present in all specimens, usually occupying a single scale row, but in one, one and a half scale rows. A fairly distinct dorsal pattern is evident of two rows of spots on each side, none fused together although all are of rather small size. There are no spots on the scales below the lateral light line (except for darkened bases of the scales). Likewise, the belly is largely unspotted.

At both the localities where *T. errans* was taken, *T. eques* is known to occur (see list of specimens of *T. eques eques* and *T. eques cyrtopsis*), despite very considerable similarities in appearance and scutellation. The differences between them, while numerous, are not major.

In 1942, this form was regarded as a subspecies of *T. ordinoides*. Although its relationships appear to be with this group, there is no real evidence or indication of intergradation. Accordingly, upon the suggestion of Dr. Henry Fitch, who kindly expressed an opinion, this form is now regarded as a distinct species. As Dr. Fitch pointed out, the maxillary tooth counts of *T. errans* and the form from which it was presumably derived (*T. o. vagrans*) are markedly different.

Further data on variation in maxillary tooth counts were obtained. All eight *T. errans* were examined, and found to have 16 to 18 maxillary teeth; the two

eques from each locality where *T. errans* is recorded were found to possess 23 to 26 maxillary teeth (No. 21 [Ciudad] 24 ; No. 26 [Ciudad] 26 ; No. 20 [Ioquiro] 25 ; No. 21 [Ioquiro] 23).

THAMNOPHIS MACROSTEMMUS MACROSTEMMUS (Kennicott).

A series of 11 specimens is available from the following localities : Hda. del Castillo, Guadalajara, Jalisco (No. 1892.10.31.26, collected by A. C. Buller) ; Mexico City, Distrito Federal (No. 1880.4.7.52, presented by P. Geddes) ; Oaxaca (Oaxaca ?) (Nos. 1881.10.31.36–40, collected by Mr. Hoege and purchased from Godman) ; Lake Xochimilco, México (Nos. 1903.9.30.188, 1940.1.11.30, both collected by Hans Gadow) ; and ' México ' (Nos. 1869.1.15.5–6, purchased from Mr. Cuming). Boulenger (1893 : 212) lists all of these specimens, except Nos. 30 and 188 which were not available to him, under *T. ordinatus macrostemma*. The remaining six specimens listed by him as *T. ordinatus macrostemma* are referred to *T. macrostemmus megalops* by us.

In scutellation all agree perfectly with the diagnostic features of this race, except that the male from Jalisco has one more caudal (79) than 93 per cent. of other specimens. The Guadalajara area is well known to be one where intergradation occurs, however, and thus the exception there is reasonable.

The Oaxaca specimens are the only ones known from that state except for one in the U.S. National Museum from Mitla. They possess a distinctive pattern in which the lateral spots are completely absent and instead narrow, discontinuous dark lines extend along the edges of the scale rows and the skin between them , the two lines on each side next to the medial border of the lateral light line are the most prominent and regular, and almost as regular are the lines on either side of the mid-dorsal light stripe. Thus the dark spots appear to be replaced by dark lines. The mid-dorsal light stripe is 3 scale rows wide. This pattern occurs in all specimens, both young and adult, and for that reason appears more constant than the peculiar patterns described for specimens from elsewhere. The Oaxaca populations therefore probably deserve recognition as a distinct race. We believe, however, that to do so would require revision of the other populations of the species, for it has long been emphasized that numerous geographic variations in pattern occur in this species

THAMNOPHIS MACROSTEMMUS MEGALOPS (Kennicott).

Seven specimens are referred to this race, from Ciudad, Durango (Nos. 1883.4.16.31-35 [6 specimens], collected by A. Forrer), and from Bocoina, Chihuahua (1940.1.11.31, collected by Hans Gadow). All, except the one from Chihuahua which was not then available, were listed by Boulenger (1893 : 212) under *T. ordinatus macrostemma*. Some of the Durango specimens (Nos. 31, 32) have very narrow mid-dorsal light stripes, which do not encroach at all upon the para-vertebral scale rows. In all the others the edges of the para-vertebrals are involved. In none is the stripe broad, however (3 scale rows or more), as is usually true of *T. m. macrostemmus*.

THAMNOPHIS MELANOGASTER MELANOGASTER (Peters).

Twelve specimens are present of this subspecies. One (No. 1903.9.30.189) is from Lake Xochimilco, Distrito Federal, collected by Hans Gadow ; three others (Nos. 1880.4.7.50–51) are from the vicinity of Mexico (City), Distrito Federal, presented by P. Geddes ; and the remainder are from unknown localities (Nos. 1864.1.15.18–19 ; 1868.3.3.47–49 [6 specimens] ; 1871.2.7.32.37). The latter two are labelled ' Tehuantepec,' and were purchased from Mr. Boucard, but unquestionably the locality is erroneously recorded. Boulenger (1893 : 225–226) listed all of these specimens under *T. melanogaster*, except No. 189, which was collected in 1903 and therefore was not available to him. The remaining four specimens listed by Boulenger as *T. melanogaster* are referred to *T. melanogaster canescens* by us.

These specimens demonstrate the fact that within the populations referred by Smith (1942 : 116–117) to *T. m. melanogaster* two subspecifically distinct groups occur : one is restricted to the Valley of Toluca (so far as present records indicate), while the other occurs in the valley of Mexico. All the specimens in the British Museum, however, appear to be typical of the easternmost race, to which the name *T. m. melanogaster* is applicable.

THAMNOPHIS MELANOGASTER CANESCENS Smith.

Five specimens represent this race. One (No. 1892.9.5.40) is from La Cumbre de los Arrastrados, Jalisco, 8,500 ft., collected by A. C. Buller ; two (Nos. 1892.10. 31.27–28) from Colonia Brizuela, Hda el Rosario, Autlán, Jalisco, collected by A. C. Buller ; one (No 1851.3.13.24) from 'Western Mexico,' purchased from Mr. Mather ; and one (No. 1897.1.11.7) from Guanajuato, sent by Alfredo Dugès. Boulenger (1893 : 226) listed Nos. 24, 27, 28 and 40, under *T. melanogaster*, while No. 7 was collected in 1897 and was not available to him. Attention is called to the fact that No. 40, listed from La Cumbre de los Arrastrados, Jalisco, 8,500 ft., is the same specimen that Boulenger lists erroneously from La Laguna, Juanacatlán, Jalisco, 6,500 ft.

All are 'typical' enough of the race, although certain variations (condition of lateral light stripe, number of postoculars) do not exhibit the percentage distribution recorded by Smith (1942 : 118, 119) for larger series. The one from Guanajuato has a belly pattern intermediate between the narrow or obsolete stripe characteristic of western *T. m. canescens*, and the extensive black marking characteristic of eastern *T. m. melanogaster*. Since it was obtained in an intermediate geographic area it is reasonable to suppose it may represent either an intergrade or an approach toward an intergrading condition.

The lateral light stripes, 'seldom evident' in other specimens, are absent in only one specimen of the present series ; in the other four the lower edge of the stripe varies, however, from a state of virtual absence to a well-defined condition. No specimen shows evidence of a mid-dorsal light line as previously observed. In one of the five the second supra-labial is in contact with the nasal : this represents a percentage (20) close to the previously recorded average (22 per cent). However, only two have 2–2 or 2–3 post-oculars, a condition previously recorded in 72 per cent. of the specimens. In the only male, the subcaudals are more than 65 (76), as they should be, while in the females all are over 55, as expected.

THAMNOPHIS MELANOGASTER LINEARIS, subsp. nov.

Holotype.—Male, E. H. Taylor—H. M. Smith Coll No. 15942, from Lerma, México, collected by E. H. Taylor and H. M. Smith.

Paratypes.—E. H. Taylor—H. M. Smith Coll. Nos. 5044–62, 5075–8, 5076A, 15943–7, with the same data as the holotype.

Diagnosis.—Distinguished from other members of the species by the reduced number of caudals in both sexes and by the presence of a mid-dorsal light line in the young and some adults. Differs from *T. m. canescens* also in the usual presence of a contact between the second supra-labial and the nasal, the well-defined lateral light stripes, the extensively blackened belly, and the larger number of post-oculars.

Description of the holotype.—A male with 2–2 pre-oculars, 3–3 post-oculars, 8–8 supra-labials, 10–10 infra-labials, 146 ventrals, 59 caudals and 19–19–17 scale rows.

Comparisons.—The present subspecies differs from all others of the species in having a vertebral light line distinct in the young and evident even in some adults. Neither of the other races exhibits such a light line at any age. It is likewise distinctive in having a reduced number of sub-caudals : 64 or fewer in males (100 per cent.) and 54 or fewer in females (93 per cent.).

The three subspecies of *T. melanogaster* may be contrasted as follows :—

Subspecies	*melanogaster*	*linearis*	*canescens*
Second supra-labial contacts nasal*	83% (12)	83% (30)	+22% (64)
Vertebral light stripe	never	+ young and some adults	never
Belly	mostly black	mostly black	+ a narrow mid-ventral dark streak, or none
Lateral light stripe	often evident	seldom not evident	seldom evident
Post-oculars 3–3 or more	70% (26)	80% (30)	+29% (84)
Male caudals 64 or less	21% (14)	+100% (14)	26% (34)
Female caudals 54 or less	20% (10)	+ 93% (15)	14% (42)

In the above table the sign (=) indicates a point of difference between the two subspecies named on either side of the line; differences between *T. m. melanogaster* and *T. m. canescens* are indicated on the left-hand side of the column for *T. m. melanogaster*. Presence of the sign + indicates that the differential character is one unique to the race named on the side where the sign is placed.

Inspection of this table reveals the curious fact that the two end races (*T. m. canescens* and *T. m. melanogaster*) are distinguished by fewer differences than separate *T. m. linearis*, the geographical intermediate, from *T. m. canescens*. Of further importance, *T. m. canescens* and *T. m. linearis* both possess certain unique characteristics (three each) while *T. m. melanogaster* possesses none.

These facts indicate that *T. m. melanogaster* represents an ancestral population from which the other two independently were derived : (1) few differences between either of the derivative and the ancestral race (three each), many between the derivatives themselves (seven) ; and (2) no unique characters in the ancestral race, several in the terminal populations. If the supposition of an ancestral position for *T. m. melanogaster* is correct, it may be assumed that the western race (*T. m. canescens*) migrated northward and thence westward, skirting the present valley of Toluca, to which *T. m. linearis* is now apparently restricted.

The scale counts given by Peters (1864 : 389) are not particularly useful for allocation of the name, inasmuch as the sex of the type is not recorded. While the extremes in the actual combination of 144 ventrals and 56 caudals have not been matched in recorded counts of any race save *T. m. canescens*, the approach is close in both other races. The type is described with 3–3 post-oculars, thus rendering the chances only 1 in 4 that it represents *T. m. canescens*. The belly is apparently black (' *melanogaster* '), and the dorsal stripe is apparently absent (' olive-colored above, with a bright indistinctly outlined band along the two lower scale rows '). These characters eliminate from reasonable possibility both *T. m. canescens* and *T. m. linearis*.

Tropidonotus mesomelanus Jan (1865 : 230–231) likewise apparently was applied to *T. m. melanogaster* (s. s.), inasmuch as the lectotype (Smith, 1942 : 116) is black-bellied and lacks a dorsal stripe. The original citation of this name (Jan, 1863 : 73) was accompanied by such an inadequate description that authors even of that date would have been unable to distinguish the species from others then known. We accordingly count the name as a *nomen dubium* (Opinions Intern. Comm. Zool. Nomencl., 126 : 21) and give it status as of the earliest date of adequate description (Jan, 1865 : 230–231). Acceptance of the 1863 date would give the name priority over *T. melanogaster* of Peters (1864).

Tropidonotus Baronis Mulleri Troschel (in Muller, 1865 : 610–611) cannot with certainty be allocated with any of the three races of *melanogaster* now recognized. Following Smith (1942 : 116) we allocate the name with *T. m. melanogaster*, of which it is thus a junior synonym, pending examination of the type.

* A 4-cornered contact of loreal, nasal and 1st and 2nd supra-labials is taken as a ' contact ' of the labial with the nasal.

THAMNOPHIS PHENAX PHENAX (Cope).

A single specimen (No. 1872.6.11.1, purchased from Mr. Cutter), is from Orizaba, Veracruz. It is a male with 19–19–17 scale rows, 73 caudals, 8–8 supra-labials, 10–10 infra-labials, 1–1 pre-oculars, 3–3 post-oculars, 1–2–3 temporals, a total length of 554 mm., tail, 133 mm.; ratio of tail to total length, 0·240; the blotches on the body are typical of the race, of large size, reaching to the outer scale rows, 44–46 on body. There is a large, light-centred dark marking on the parietals, as is typical.

This specimen is the one listed by Boulenger (1893 : 210) as *T. ordinatus phenax*.

THAMNOPHIS RUFIPUNCTATUS (Cope).

Three juveniles (Nos. 1911.12.12.22–24) are from Ioquiro, Sierra Tarahumare, Chihuahua, collected by Mr. Neilly and purchased from H. Gadow. Since these specimens were collected in 1911, Boulenger (1893) did not include them in his work These do not extend the known geographic range, but are noteworthy by extending the limits of known variation (cf. Smith, 1942, and Smith and Mittleman, 1943) in ventral counts of Mexican females (from a maximum of 160 to 162) and in caudal counts of Mexican males (from a minimum of 76 to 75), and in providing a further example of the rare variation in which two supra-labials enter the orbit. The pattern is of well-defined spots in all three rows on each side of the dorsum, and with small spots on the anterior ends of the ventrals; this appears to be more or less 'typical' of the species, although it does not, unfortunately, well match in dorsal pattern the peculiar spotless condition of the type of *rufipunctatus*.

THAMNOPHIS SAURITUS CHALCEUS (Cope).

Ten specimens of this race are in the collection from the following localities: Los Cuadros de San Pedro, Costa Rica (No 1913.7.19.140, collected by Underwood and presented by F. D. Godman); 'Honduras' (no No.); Belize, British Honduras (No. 1857.12.15.1, two specimens, collected by J. Smith); Cozumel Island, Yucatán (Nos. 1886.4.15.21–22, collected by Gaumer), Jalapa, Veracruz (Nos. 1893.1.9.17, collected by F. D. Godman; No. 1860.12.18.37, purchased from Mr. Cuming; and No. 1881.10.31.45, collected by Mr. Hoege); and Río Atoyac, Veracruz * (No 1893.1.9.16, collected by H. H. Smith and presented by F. D. Godman). Boulenger (1893 : 213–214) lists Nos. 1 (two specimens), 16, 17, 21, 22, 34, 45, and the specimen from 'Honduras' under *T. saurita*. No. 10 was collected in 1913 and was therefore not available to him.

The scale counts, as well as other features, of this series appear to be within the normal range of variation with the possible exception of the ventrals which number 144 in one male (149 the previous known minimum).

THAMNOPHIS SAURITUS PROXIMUS (Say).

A single specimen (No. 1861.8.15.68), presented by the Smithsonian Institution, is in the collection. Boulenger (1893 : 213) listed this specimen under *T. saurita*. Nine other specimens from Mexico and Central America listed under *T. saurita* by Boulenger are referred to *T. sauritus chalceus* by us, while thirteen of his specimens were not from Mexico.

This specimen is a male with 19–19–17 scale rows, 168 ventrals, 106 caudals, 8–8 supra-labials, 10–10 infra-labials, 1–1 pre-oculars, 3–3 post-oculars, 1–2–3 or 1–3 temporals, 700 mm. in total length, 211 mm. in tail length, and a total tail length ratio of 0·301.

THAMNOPHIS SCALARIS SCALARIS Cope.

Two specimens are in the collection: one (No. 1903.9.30.187) between Xomitla and La Barbara, Veracruz, collected by Hans Gadow, and the other (No. 1881.10.

* Stated 'Guerrero,' but almost certainly in error.

31.41) from ' Oaxaca,' collected by Hoege. Specimen No. 41 is described by Boulenger (1893 : 204) as *T. scalaris*. No. 187 was collected in 1903 and therefore was not included by Boulenger. The other seven specimens referred by him to *T. scalaris* are here regarded as *T. s. scaliger*. Specimen No. 41 definitely cannot be referred to *T. s godmani*, the subspecies to be expected in the Oaxaca area. If indeed the locality is correctly stated this (1) would constitute the only record for *T. s. scalaris* known from the isolated southern portion of the plateau, and (2) would require re-evaluation of the facts bearing upon the subspecific status of *T. s. godmani*. We strongly doubt the actual occurrence of *T. s. scalaris* in the Oaxaca area, however, in spite of the Hoege specimen, since the fairly extensive collecting there and in Guerrero (which has a strikingly similar fauna in the uplands) has not produced other specimens. It seems much more probable that the specimen, which with one exception does not deviate from previously established limits of variation in *T. s. scalaris*, is from eastern Mexico—perhaps the Veracruz area, where this subspecies is commonly found, and where Hoege did secure *T. chrysocephalus*. Both forms occur at Jalapa, where the latter was taken. The one peculiarity of the specimen is the very low ventral count, which at 130 is 3 less than the next lowest recorded in the entire species.

Characteristics of these two specimens, respectively, are as follows : scale rows, 17–17–15, 17–19–15 : ventrals 148, 130 : caudals 60 (♂), 76 (♂) ; supra-labials, 7–7, 7–7 ; infra-labials 8–9, 9–9 ; pre-oculars 1–1, 1–1 ; post-oculars 3–3, 2–3 , total length 415 mm., 381 mm. , tail length 100 mm., 125 mm. ratio of tail to total length 0·241, 0·328.

THAMNOPHIS SCALARIS GODMANI (Gunther).

Ten specimens are in the museum, all from Omiltemc, Guerrero. None of these was available to Boulenger in 1893. Six (not examined) are cotypes, now 1946.1.21. 80–85. One of the original cotype series was sent in 1929 in exchange to the Museum of Comparative Zoology (now No. 28466). All the cotypes were collected by H. H. Smith and purchased from F. D. Godman. Two (1906.6.1.247–248) were collected by Hans Gadow, and two (1894.11.14.16, 19) were presented by F. D. Godman. This subspecies is very easily confused with *T. chrysocephalus* and is most easily distinguished by the characters mentioned in the discussion of the latter species.

Only the four specimens not cotypes were examined. The variation in their characters falls within known limits.

THAMNOPHIS SCALARIS SCALIGER (Jan).

Eleven specimens are present, as follows : Mexico City, Distrito Federal (No. 1868.4.7.10), collected by Doorman : Lake Xochimilco, México (No. 1903.9.30. 193), collected by Hans Gadow : La Cumbre de los Arrastrados, Talpa Mascota, Jalisco (Nos. 1892.10.31.20–22, 1892.9.5.39), collected by A. C. Buller : Colonia Brizuela, Hda. el Rosario, Autlán, Jalisco (1892.10.31.23–25), collected by A. C. Buller ; Tancítaro, Michoacán (No. 1914.1.28.125) ; and ' southern Mexico ' (No. 1893.1.9.4), presented by F. D. Godman. These provide records of no new localities of occurrence, although they extend somewhat the known limits of variation. Boulenger (1893 : 203–204) lists Nos. 4 and 10 above under *T. scaliger*, Nos. 20, 21, 22, 23, 24, 25 and 39 under *T. scalaris*, while Nos. 193 and 125 were not available to him.

The British Museum specimens combined with those recorded by Smith and Laufe (1945 : 352) require revision of Smith's table (1942 : 104) to appear as follows :—

	scaliger	*scalaris*	*godmani*
Posterior scale rows less than 17	3% (1 in 31)	68% (25 in 37)	100% (22)
Maximum scale rows 19	100% (31)	84% (32 in 38)	5% (1 in 22)
Anterior scale rows 17	13% (4 in 31)	86% (32 in 37)	100% (22)
Caudals in males more than 60	50% (6 in 12)	95% (18 in 19)	100% (18)
Ventrals in males 143 or more	50% (6 in 12)	10% (2 in 20)	89% (17 in 19)
Infra-labials 10 or more on each side ..	32% (10 in 31)	24% (9 in 38)	73% (16 in 22)

THAMNOPHIS SUMICHRASTI FULVUS (Bocourt).

Two specimens (Nos. 1860.12.1.28–29), collected by O. Salvin at Dueñas, Sacatepequez, Guatemala, are apparently typical of this highland race. In both the pattern is extremely obscure, and the mid-dorsal stripe only feebly indicated. There are no belly marks. The dark labial borders are very narrow.

Boulenger (1893 : 209) lists No. 28 under the subspecies *T. ordinatus eques*, while the other is listed under *T. o. sumichrasti*.

The two specimens, both females, mentioned above vary respectively as follows : scale rows 19–19–17, 19–19–17 ; ventrals 145, 144 ; caudals 62, 61 ; supra-labials, 8–8, 8–8 ; infra-labials 10–10, 10–10 ; pre-oculars 1–1, 1–1 ; post-oculars 3–3, 3–3 ; total length 730 mm., 892 mm. ; tail length 160 mm., 175 mm. ; ratio of tail to total length 0·219 0·196.

THAMNOPHIS SUMICHRASTI SALVINI, subsp. nov.

Holotype. Brit. Mus. No. 1869.2.22.3 from Rio Chixoy below the town of Cubules (? Cubilguitz), Guatemala, collected by O. Salvin.

Paratype. Brit. Mus. No. 1860.12.1.24 from 'Guatemala,' same collector. Boulenger (1893 : 209) lists both of these specimens under *T. ordinatus eques*.

Diagnosis. A member of the *eques* complex distinctive through combination of the following characters : no dark belly spots ; labial bars very narrow ; anterior spots on sides of body (exclusive of nape spots) not fused ; mid-dorsal stripe one scale row wide, very prominent ; ventrals few, 135 to 152 in females ; sub-caudals 91 in sole known specimen with complete tail.

Description of holotype. Female : Supra-labials 9-9, the rear one abnormally subdivided ; 4th and 5th labials entering orbit ; pre-oculars 1–1 ; post-oculars 3–3 ; temporals 1 (2)–2 (an abnormal scale split from parietal opposite the first temporal on one side) ; infra-labials 10–10 ; anterior chin-shields shorter than posterior ; latter completely separated from each other.

Dorsal scales in 19–19–17 rows, the fourth row dropping on each side at the 89th ventral ; tail incomplete, sub-caudals 79 on portion present (an estimated 10 missing). Total length 857 mm. ; tail 216 mm. ; ratio of tail to total length 0·252.

Head uniform light olive above and on sides, except for narrow dark margins on the rear of supra-labials 3 to 7 inclusive ; nuchal spots somewhat diffuse, fused medially ; mid-dorsal light stripe very prominent, one scale row wide, not encroaching upon paravertebral rows ; lateral light stripes poorly defined, on second and third scale rows ; two rows of alternating spots on each side between lateral and mid-dorsal light stripes ; these spots rather large (covering an area of some four scales), but chiefly evident on the skin between the scales, and rather obscure on those portions of the body from which the skin has not been shed ; a small black spot on lower edge of alternate (usually) spots, often involving extreme lateral edge of ventrals ; extreme anterior edge of ventrals black.

Variation.—The paratype is also a female with 19–19–17 scale rows, 135 ventrals, 91 caudals, 8–8 supra-labials, 10–10 infra-labials, 1–1 pre-oculars, 3–4 post-oculars, 1–2 temporals ; total length 635 mm. ; tail 200 mm. ; ratio of tail to total length, 0·315. Its pattern is almost precisely like that of the holotype.

Remarks.—The paratype apparently was taken somewhere on the Atlantic slopes of Guatemala, since it was secured on the 1859–1860 trip made by Salvin to Dueñas, San Gerónimo, Cobán, and other localities in Alta and Baja Vera Paz. He did not reach Pacific slopes on that trip, except perhaps at Dueñas, where a different race of *T. sumichrasti* occurs (*T. s. fulvus*). Therefore, the association of the paratype with the holotype is reasonable for geographical as well as morphological reasons.

These specimens are the only ones of the species recorded from specific areas in the Atlantic foothill area of Guatemala. *T. s. fulvus*, a nearly stripeless form, is restricted to the highlands ; *T. s. cerebrosus*, with a wider dorsal stripe, fewer sub-caudals and perhaps fewer labials, is from Pacific slopes ; *T. s. praeocularis*, with

prominent head markings, a wide mid-dorsal stripe, fewer caudals, large anterior blotches on sides of body, and paired belly spots, is restricted to the Yucatán Peninsula and undoubtedly (not yet recorded) occurs in northern Guatemala. But no specimens have been recorded definitely, other than the present, from the area between the ranges of *T. s. praeocularis* and *T. s. fulvus*. A factor contributing to the complexity of the situation, however, is the occurrence of *T. s. sumichrasti* in the Atlantic foothills of Chiapas, and in Nicaragua—all presumably the same. There is even a ' Guatemala ' record (U.S. Nat. Mus.). The only place for this race to occur in Guatemala, if it actually does so, is somewhere in the area between the Yucatán Peninsula and the highlands of the plateau—the area from which the present specimens were taken. These cannot be considered intermediate between *T. s. sumichrasti* and any of the other striped races. Accordingly, either both forms (*T. s. sumichrasti* and *T. s. salvini*) occur in the area prescribed, or a hiatus in that area occurs in the range of the former race. Only further material will elucidate the problem.

T. s. salvini bears the closest resemblance to *T. e. eques* of all the Central American (i.e. exclusive of Mexico) races. It differs from all others of its species in caudal count, and from *T. eques* in lack of belly spots and in reduction of the labial bars. The speculation that it is the Central American counterpart of *T. eques*, from which the other races of *T. sumichrasti* evolved, is tempting. On the other hand, it may simply be a parallel development rather than the remnant of an ancestral stock once united with *T. eques*.

Specific Allocation.—The correct specific arrangement of the several races assigned by Smith (1942) to the species *T. eques* and *T. sumichrasti* is not yet determined. Obviously more material, especially from Veracruz, is needed before this can be done. Bogert and Oliver (1945) present arguments (not all of which appear valid to us) in support of the combination of all in a single species, *T. eques*. With no new facts to present, we can see little merit in further discussion of the problem, which obviously needs further new work. New considerations should not, however, overlook (1) the apparent existence of separate centres of dispersal in Guatemala (*T. sumichrasti*) and Mexico (*T. eques*), nor (2) the apparent divergence (not convergence) of geographically adjacent terminal races of each group.

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Variation in *T. chrysocephalus*

Number.	Sex.	Scale rows.	Ventrals.	Caudals	Supral	Infral	Preoc.	Postoc	Total length	Tail length.	Ratio tail. total length
93.1.9.8	♀	17-17-15	152	70	8-8	10-10	1 1	3 3	555	130	0·234
81.10.31.58	♂	17-17-15	150	69	8 8	10 10	1-1	3-3	245	55	0·224
93.1.9.5	♂	17-17-15	151	81	8-8	10 10	1 1	3 3	370	140	0·271
93.1.9.7	♂	17-17 15	142	77	8-8	9 10	1 2	3-3	300	135	0·270
93.1.9.6	♂	17-17-15	146	75	8 8	10 10	1 1	3-3	350	90	0·257
94.11.14.17	♂	17-17 15	144	74	8 8	10 10	1 1	3 3	264	62	0·235
1906.6.1.249	♂	17 17 15	144	76	8 8	10 10	1 1	3 3	245	65	0·265

Variation in *T. e eques*

Number.	Sex.	Scale rows	Ventrals	Caudals	Supral	Infral	Preoc	Postoc	Total length	Tail length	Ratio tail total length
92.2.8.53		19-			7 7	10 10	1 1	3 3	-		
85.6.20.1		19 19 17	153		8 8	10 10	1 1	3 3	216	-	-
94.3.1.10		19 19-17	144	80	8 8	10 10	1 1	3 4	282	70	0·248
92.2.8.54		19 19 17	158	89	8 8	10 10	1 1	3 3	364	95	0·261
93.1.9.13		19 19-17	150	75	7 7	10- 9	1-1	4 4	534	140	0·262
93.1.9.14		19-19 17	146	74	8-8	10 10	1 1	3 4	625	158	0·253
93.1.9.12		19-19-17	150	83	8 8	10-10	1 1	3 3	626	165	0·263
92.1.9.10		19 19-17	174	75	7 7	11-10	1 1	3-3	662	150	0·227
82.11.15.26		19-19-17	158	101	8 8	10-10	1 1	3 3	720	202	0·281
81.10.31.59 . .	♂	19-19-17	163	94	8 8	10-10	1-1	4-4	245	64	0·261
82.11.15.21 . ..	♂	20 19-17	160½	91	8 8	10-10	1-1	2-2	443	123	0·278
92.1.9.9	♂	19-19-17	155	77	7-7	10-10	1 1	3-3	524	132	0·252
93.1.9.11	♂	19-19-17	154	92	8 8	10-10	1 1	3 2	543	153	0·282
93.1.9.15	♂	19 19 17	157	87	8 8	10-10	1 1	4-4	549	152	0·277

Variation in *T. errans*.

Number.	Sex	Scale rows	Ventrals.	Caudals	Supral	Infral	Preoc	Postoc	Total length.	Tail length.	Ratio tail total length.
1882.11.15.29		19-19 17	147	74	7 7	10 9	1 1	3-3	418	100	0·239
1882.11.15.23 .. .		19-19-17	150		7 7	10- 9	1 1	3 3	414		--
1911.12.12.20	♂	19-19-17	160	86	7 7	10-10	1 1	3-3	516	135	0·262
1882.11.15.27	♂	19-19-17	159	82	7 7	10 10	1 1	3 3	513	143	0·279
1882.11.15.28	♂	19-19-17	153	82	7-8	10-11	1-1	3-3	492	135	0·274
1882.11.15.25	♂	19-19-17	160	85	7 7	10-11	1-1	3-3	400	99	0·248
1882.11.15.24	♂	19-19-17	148	85	7 7	10-10	1 1	3-3	337	90	0·267
1882.11.15.22	♂	19-19-17	163	82	7-7	10-10	1 1	2-3	303	74	0·244

Variation in *T. m. macrostemmus*.

Number.	Sex.	Scale rows.	Ventrals.	Caudals.	Supral	Infral.	Preoc.	Postoc.	Total length	Tail length.	Ratio tail total length.
1881.10.31.39	♂	21 21-17	156	-	8-9	10-10	1 1	3 3		—	-
1903.9.30.188	♂	21-22-17	160	63	8-8	10-10	1 1	3-3	256	53	0·207
1869.1.15.5		21-21-17	156	68	8-8	10-10	1-1	4-4	392	87	0·222
1881.10.31.27		21-21-17	156	70	8 8	10-10	1 1	3-3	590	132	0·224
1881.10.31.40	♂	20-20-17	153	67	8-8	10-10	1-1	3-3	671	145	0·216
1869.1.15.6		21-21-17	155	63	8-8	10-10	1-1	3-3	676	148	0·219
92.10.31.26	♀	21-21-17	166	79	8-8	10-10	1 1	3-3	210	49	0·233
81.10.31.36	♀	21-21-17	166	77	8-8	10-10	1 1	3-3	292	65	0·223
80.4.7.52	♀	21-21-17	165	77	8-8	10-10	1 1	3-3	301	70	0·233
81.10.31.38	♀	19-19-17	156	72	8 8	10-10	1 1	3-3	466	100	0·215
1940.1.11.30	♀	20 21-17	149	61	8 8	10 10	1 1	3-3	510	109	0·214

Variation in *Thamnophis m. megalops*.

Number.	Sex	Scale rows	Ventrals	Caudals.	Supral.	Intral	Preoc	Postoc.	Total length	Tail length.	Ratio tail total length.
83.4.16.35	♂	21-21 17	160	66	8 8	10-10	1-1	3 4	404	85	0·210
83.4.16.31	♂	21-21-17	160	63	8-8	9-10	1 1	2-2	505	105	0·208
1940.1.11.31	♀	20-21-17	158	-	8-8	10 10	1-1	3-3	-	-	
83.4.16.32	♀	21-21-17	169	74	8-8	9-10	1-1	2 3	484	98	0·202
83.4.16.33	♀	21-21-17	163	79	8 8	10-10	1-1	3 3	523	128	0·245
83.4 16.34	♀	21-21-17	171	83	8-8	10-10	1 1	3 3	652	153	0·235
83.4.16.36	♀	21 21 17	167	79	8 8	?-10	? 1	? 3	676	155	0·229

Variation in *T. m. melanogaster*.

Number.	Sex.	Scale rows.	Ventrals.	Caudals	Supral.	Infral	Preoc.	Postoc.	Total length	Tail length.	Ratio tail total length.
68.3.3.49A		19-19-17	148	57	8-8	10-10	2-2	2-2	354	72	0·203
80.4.7.51		19-19-17	147	57	8-8	10-10	2 2	2-3	475	103	0·217
64.1.15.18		19-19-17	147	55	8 8	10-10	2 2	2 2	525	110	0·209
80.4.7.51A	♂	19-19-17	155	65	8-8	10-10	2-2	3-3	219	48	0·214
68.3.3.48	♀	19-19-17	154	62	8-8	10-10	2-2	3-3	425	98	0·230
71.2.7.32	♀	19-19-17	158	68	8 8	10-10	2 2	3-3	431	105	0·241
71.2.7.37	♀	19-19-17	155	65	8-8	10-10	2-3	3-3	452	107	0·232
64.1.15.19	♀	19-19-17	154	68	8-8	10-10	2-3	3-3	508	121	0·238
80.4.7.50	♀	19-19-17	153	65	8-8	10-10	2-2	3 3	512	124	0·242
68.3.3.40	♀	19-19-17	149	67	8-8	10-10	2-2	3-3	520	130	0·250
1903.9.30.189	♀	19-19-17	149	58	8-8	10-10	2-2	3-3	532	118	0·221
68.3.3.47	♀	19-19-17	156	71	8-8	9-10	2-2	3-3	569	142	0·249

VARIATION IN *T. m. canescens*.

Number.	Sex	Scale rows	Ventrals	Caudals	Supral	Infral	Preoc	Postoc	Total length	Tail length	Ratio tail total length
51.3.13.24	♀	19–19–17	139	65	8–8	10–10	2–2	2–2	182	43	0·236
97.1.11.7		19–19–17	142	57	8–8	10–10	2–2	2–2	389	87	0·222
92.9.5.40		19–19–17	139	71	8–8	9–10	2–2	3–3	592	143	0·241
92.10.31.27		19–19–17	145	64	8–8	10–10	2–2	3–3	600	134	0·223
92.10.31.28	♂	19–19–17	146	76	8–8	10–10	2–2	3–3	208	55	0·264

VARIATION IN *T. rufipunctatus*.

Number.	Sex.	Scale rows.	Ventrals	Caudals	Supral	Infral	Preoc	Postoc	Labials enter eye	Total length	Tail length.	Ratio tail total length
1911.12.12.24		21–21–17	162	66	8–8	10–10	2–2	2–3	4, 5–4, 5	211	45·0	0·213
1911.12.12.23		21–21–17	161	70	8–8	10–10	3–3	3–3	4–4	210	50·0	0·238
1911.12.12.22	♂	19–21–17	167	75	8–8	10–11	2–2	3–3	4–4	225	51·5	0·229

VARIATION IN *T. sauritus chalcops*

Number	Sex.	Scale rows	Ventrals	Caudals	Supral	Infral	Preoc	Postoc	Total length	Tail length	Ratio tail total length
93.1.9.16		19–19–17	151		8	10–10	1–1	3–3			
57.12.15.1		19–19–17	145		8–8	10–10	1–1	3–3			
93.1.9.17		19–19–17	154		8–8	10–10	1–1	3–3			
86.4.15.22		19–19–17	149	71	8–8	10–10	1–1	3–3	585	147	0·251
No number		19–19–17	145	91	8–8	10–10	1–1	3–3	671	205	0·305
1913.7.19.140		19–19–17	153	92	8–8	10–10	1–1	4–4	710	209	0·294
57.12.15.1A	♂	19–19–17	144	95	8–8	10–10	1–1	3–3	212	93	0·439
81.10.31.45	♂	19–19–17	158	93	8–8	10–10	1–1	2–3	307	90	0·293
60.12.18.37	♂	19–19–17	154	92	8–8	10–10	1–1	3–3	487	145	0·298
86.4.15.21	♂	19–19–17	149	92	8–8	10–10	1–1	3–3	501	149	0·297

VARIATION IN *T. s. godmani*

Number.	Sex.	Scale rows	Ventrals.	Caudals	Supral	Infral	Preoc	Postoc	Total length	Tail length	Ratio tail total length
1906.6.1.248		17–17–15	143	73	7–7	10–10	1–1	3–3	580	145	0·250
94.11.14.16		17–17–15	143	62	7–7	10–10	1–1	3–3	228	53	0·232
1906.6.1.247	♂	17–17–15	146	81	7–7	10–10	1–1	3–3	590	150	0·254
94.11.14.19	♂	17–17–15	142	79	7–7	10–9	1–1	3–3	228	64	0·280

VARIATION IN *T. s. scaliger*.

Number.	Sex.	Scale rows.	Ventrals.	Caudals.	Supral.	Infral.	Preoc	Postoc	Total length.	Tail length.	Ratio tail/total length.
1892.10.31.21	♀	17–19–17	139	52	7–7	9–9	1–1	3–3	—	—	—
1903.9.30.193	♀	19–18–17	137	43	7–8	9–9	1–1	2–2	279	47	0·168
1892.10.31.20	♀	19–19–17	142	59	7–7	9–10	1–1	3–3	362	73	0·202
68.4.7.10	♀	19–19–17	144	47	7–7	9–9	1–1	2–3	374	66	0·176
1914.1.28.125	♀	19–19–17	145	52	7–7	9–10	1–1	3–3	482	96	0·199
1892.10.31.23	♀	19–19–17	142	60	7–7	9–9	1–1	3–3	552	124	0·225
1893.1.9.4	♂	18–19–17	152	55	7–7	9–10	1–2	2–2	370	75	0·203
1892.10.31.24	♂	19–19–17	139	65	7–7	9–9	1–1	3–3	388	99	0·255
1892.9.5.39	♂	18–19–17	139	67	7–7	9–9	1–1	3–3	394	101	0·256
1892.10.31.25	♂	18–19–17	139	65	7–7	9–9	1–1	3–3	428	118	0·276
1892.10.31.22	♂	17–19–17	137	65	7–7	9–9	1–1	2–3	459	121	0·264

The Interorbital Septum in Mammals.

By R. WHEELER HAINES, D.Sc., Department of Anatomy, Faculty of Medicine, Abbassia, Cairo.

(With 40 figures in the text.)

INTRODUCTION

In most living reptiles a thin sheet of cartilage, which may be calcified, separates the orbits from each other, and in birds a sheet of bone occupies the same position and is a conspicuous feature of the skull (Bellairs, 1949). In mammals (Gaupp, 1900) recognized the region of the central stem of the chondrocranium that lay between the nasal capsules anteriorly and the pituitary region posteriorly as the morphological equivalent of the reptilian interorbital septum, but he did not realize that typical well-developed septa could be found in mammals. Fischer (1903), however, found such a structure in a late embryo of an Old-World monkey, *Semnopithecus*, and figured his discovery side by side with a figure of the lizard *Lacerta* from Gaupp's monograph to demonstrate the morphological identity of the septa.

Voit (1909) found the septum in the late embryo of the rabbit, and other workers have described it in a number of different animals. de Beer and Woodger (1930) studied its early development in the rabbit, and reviewed the work of previous authors. They classified this material according to the strong, feeble or non-development of the septum, and concluded (p. 403) that the only mammals in which it was well developed were the primates and rodents, and this conclusion is repeated in de Beer's book on the skull (1937). In the present paper the distribution of the septum will be reconsidered, and it will be suggested that as regards this feature the ungulates have as good a claim as the rodents to be classed with the primates.

The significant gaps in our knowledge relate, however, not to the chondrocranium of the embryo but to the skull of the adult. The monographs which deal in detail with particular types hardly mention the matter, and Muller (1925), who wrote on the orbito-temporal region of the adult skull, knew the typical septum only in primates and rodents. The well-developed septa of the smaller deer and antelopes and of some carnivores seem to have escaped the notice of morphologists altogether, those of the eared seals have been misunderstood, and illustrations designed to show the structure of the septa are not available anywhere in the literature.

The purpose of the present paper is to describe and illustrate the position and structure of the adult septum in all groups of mammals known to possess one, to compare its adult form with that in the chondrocranium where the latter has been studied, and to consider its morphological and phylogenetic significance*.

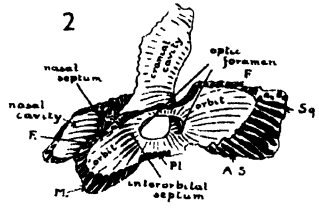
LAGOMORPHA AND RODENTS.

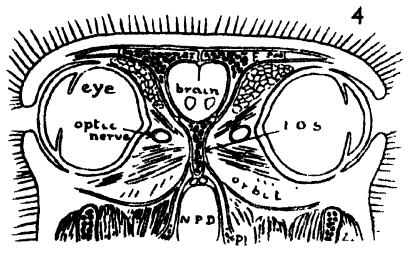
The rabbit, *Oryctolagus cuniculus*, has a small but typical interorbital septum, and since it is a readily available form whose structure and development have been exhaustively studied, this animal may be chosen to illustrate the subject. A side view of the skull (fig. 1) shows the orbit bounded above by the frontal, anteriorly by the lachrymal and maxilla, below by the zygomatic (fused with the maxilla), and the zygomatic process of the squamosal, while posteriorly the orbit is confluent with the temporal fossa. The bones mentioned build the interior walls of the orbit with the help of the palatine and alisphenoid below, and in the deepest part of the orbit there is a wide exposure of the presphenoid, with the basisphenoid just visible. (The term 'presphenoid' is used to denote the bone in the adult skull, separate in most mammals, which is usually ossified from presphenoid and orbitosphenoid centres. It corresponds to the 'presphenoid part' of the sphenoid bone of man.)

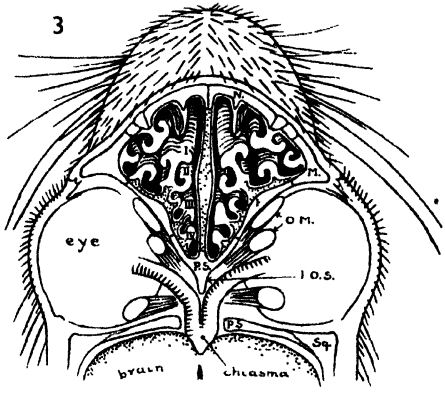
* This paper forms the second part of an investigation of the interorbital septum in amniote vertebrates originally begun in collaboration with Dr. A. d'A. Bellairs of the Dept. of Anatomy, London Hospital Medical College. Owing to the departure of the present writer to Egypt, it has not been possible to continue the collaboration and the Sauropsida and Mammalia have been dealt with separately. Conditions in Sauropsida have been described by Bellairs (1949).

The optic foramen lies in the presphenoid, leading from the cranial cavity to the orbit. Anteriorly the right and left foramina have a common boundary, a relatively thin edge of bone, the posterior margin of the interorbital septum. This septum can be demonstrated very clearly by illuminating one orbit so that the light shines through the thin septum and can be seen from the other. In the rabbit the septum is not very extensive and is entirely confined to the presphenoid bone

An isolated presphenoid from a young animal (fig. 2) shows the two lesser wings posteriorly, the optic foramma meeting at the interorbital septum centrally, and the anterior extensions which help to build the wall which separates the orbit from the nasal cavity Between these extensions the presphenoid passes a short distance into the nasal septum







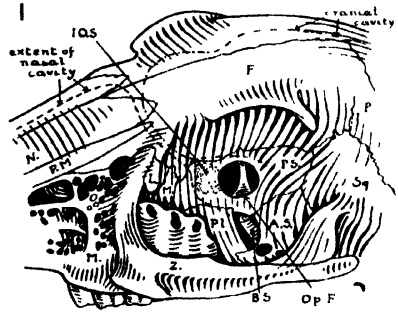


FIG. 1. *Oryctolagus cuniculus*, dry skull.
FIG. 2. *Oryctolagus cuniculus*, presphenoid bone.
FIG. 3. *Oryctolagus cuniculus*, decalcified head, horizontal section.
FIG. 4. *Oryctolagus cuniculus*, decalcified head, coronal section.

A decalcified head dissected from above down to the level of the optic chiasma shows the main relationships of the presphenoid very clearly (fig. 3). The lesser wings separate the cranial cavity from the orbit. The portion of the cranial cavity between the optic foramina is entirely occupied by the optic chiasma and the terminations of the optic nerves, which here lie side by side. Followed forwards the nerves suddenly diverge, passing through the optic foramina on either side of the interorbital septum. The septum continues forwards to meet the anterior expanded part of the bone which separates the nasal capsule from the orbit, and thus separates the optic chiasma behind from the nasal cavity in front.

A coronal (transverse) section (fig. 4) from another decalcified head shows the septum between the orbits as a bony sheet. Below it is rounded, and the two palatines which support the sides of the nasopharyngeal duct articulate with it. Above, it carries two small wings, poorly developed here, which support the brain and articulate with the frontals.

To revert to the dry skull (fig. 1), the outlines of the cerebral and nasal cavities may be marked in on the surface of the bones. (This is accomplished by shining a light into each cavity in turn, and marking the areas of translucency on the surface, checking the result on broken skulls.) It can then be seen that the interorbital septum is a bony partition between the orbits, bounded above by the cranial cavity, behind by the part of that cavity that lodged the chiasma, anteriorly by the nasal cavity with its ethmoturbinal apparatus and below by the naso-pharyngeal canal. These relationships will be found to hold generally throughout the Mammalia, but where the chiasma lies just posterior to the nasal cavity, or the cranial cavity just above the respiratory passage no septum is developed.

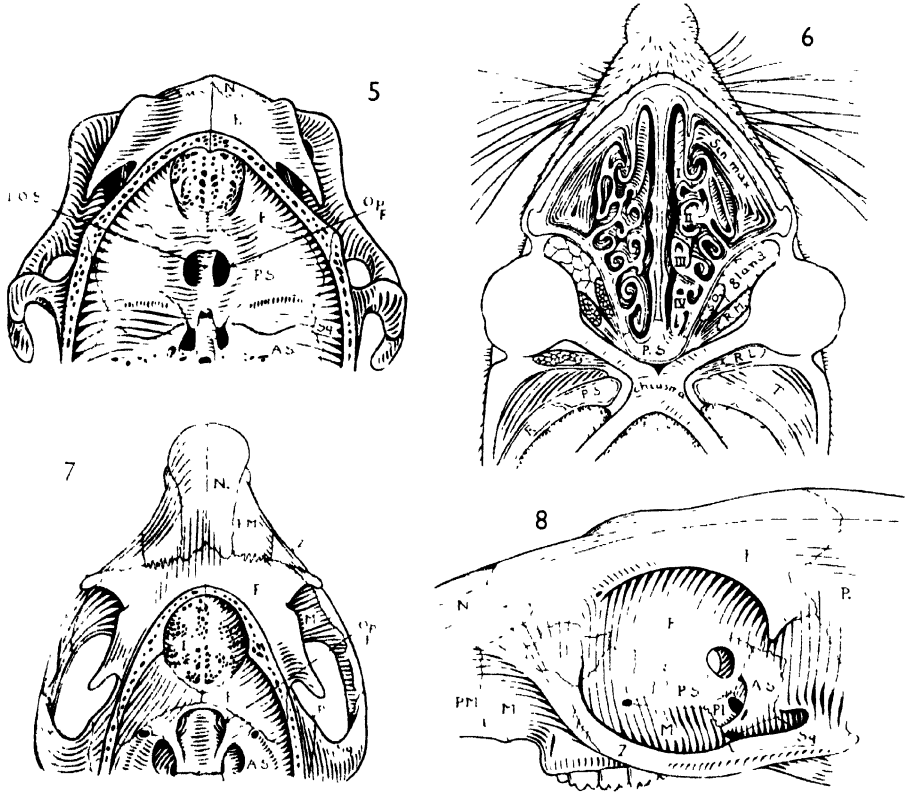


FIG. 5.- *Oryctolagus cuniculus*, skull base.
FIG. 6. *Sciurus caroliensis*, decalcified head, horizontal section.
FIG. 7.- *Sciurus caroliensis*, skull base.
FIG. 8. *Nesus setosus* (Camb. E. 1530), dry skull.

The floor of the cranial cavity viewed from above (fig. 5) shows the septum as a relatively narrow ridge of bone between the optic foramina. A glance at a skull base, or even inspection through the foramen magnum, is usually sufficient to determine the presence of a septum in any animal, for if the optic nerves split round a narrow edge of bone that edge belongs to a septum, whereas if, as is more usual, the foramina are far apart, no septum can be present.

Such a condition is illustrated among rodents by the squirrel (*Sciurus*), for here the chiasma is X shaped, and the two optic foramina are separated by a wide interva

(figs. 6 and 7). There is no trace of an interorbital septum, and the two foramina cannot be said to have a common anterior boundary. The chiasma is set directly against the bony covering of the nasal cavity, and a hole cut in the cranial floor between the optic foramina leads to the recess of that cavity, which contains the fourth ethmoturbinal. These two animals, the rabbit and the squirrel, exemplify the two common mammalian conditions in this region.

In other rodents the septum is usually absent, but in *Xerus setosus*, a relative of the squirrel, there is a septum which involves not only the presphenoid but also the frontal, so that the suture between the two bones crosses the septum (fig. 8). In *Xerus erythropus* (Camb. E. 1528) the septum is similar, but does not involve the frontal. In *Rhinosciurus*, which like *Xerus* has a long narrow skull, there is a good septum, but in most Sciuridae the skull is short and there is no septum.

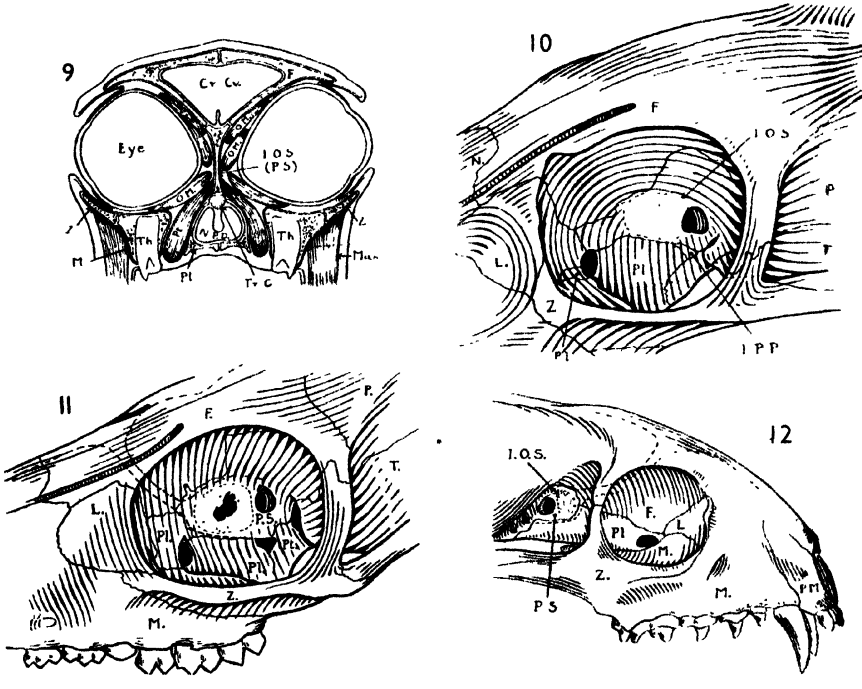


FIG. 9. *Neotragus pygmaeus* (Zool. Soc.), decalcified head, coronal section.
FIG. 10. *Cephalophorus coeruleus* (Camb. H. 21621), dry skull.
FIG. 11. *Tragulus stanleyanus* (Camb. H. 14971), dry skull.
FIG. 12. *Herpestes griseus* (London Hospital Medical College), dry skull.

Among the Muridae the musquash (*Ondatra zibetheca*) has a septum which may be perforated in the dry skull (Camb. E. 2810), or may be solid (Thos. 94), but other genera (*Mus*, *Neotoma*, *Arvicola*, *Hydromys*, etc.) have none, neither are septa known in other groups of rodents.

UNGULATES.

Septa have not previously been recorded in adult ungulates, but several of the smaller species possess them. The royal antelope, *Neotragus pygmaeus*, the smallest ungulate known, has an extensive presphenoidal septum, better developed than in any other animal outside the primates (fig. 9). The eyes and orbits are, as in

most ungulates, large, and the size of the septum is associated with the requirements of packing such large objects into a small skull. Similar septa are found in the related dik diks, *Modoqua saltiana* (Camb. H. 22.242), and *M. phillipsi* (H. 22,281).

The blue buck, *Cephalophorus coeruleus* (fig. 10), has a septum occupying the whole height of the presphenoid between the frontal and palatine articulations, and it is similar in *C. niger* (Camb. A. 47 L) and *C. harveyi* (H. 21,381). The common duiker, *C. grimmi* (H. 21,796), is larger than the other members of the genus, and here the presphenoid is reduced in height and the septum small.

In the chevrotains (*Tragulus*) there is a septum which is usually perforated by a jagged fenestra in the dry skull (fig. 11), but presumably this is filled in by membrane in the living animal. The perforation is inconstant, for in a skull of *T. javanicus* (Camb. H. 15,018) there is no fenestra in the well developed septum. In the related musk deer, *Moschus moschiferus* (Camb. H. 15,312), there is no septum, though the optic foramina are still near together, so that this form provides a transition to the usual septum-less condition of the larger deer and antelopes and of other groups of ungulates.

Carnivores and Seals

In adult carnivores again the interorbital septum has not previously been recorded, but it is found as a distinct thin bony sheet in several Mongotidae and Viverridae. In *Herpestes* it is best developed in the smaller, long headed forms (fig. 12), whereas it is poorly developed in the large, stoutly built forms such as *H. brachyurus* (B.M. 21. 10.2.21). It is found in most individuals of *Helogale*, such as *H. victorina* (13.10.18.46) and *H. rufula* (16.1.15.7), but may be absent in the latter species (16.1.15.9). A broken skull of *Cynictis penicillata* (fig. 13) in the British Museum shows the relationships to the optic foramina, the cranial cavity, the posterior extension of the nasal cavity, and the naso-pharyngeal passage. The septum occurs in other species of *Cynictis* and in *Suricata* (2.9.1.26), and there is some indication of its presence in *Atilax* (1938.5.26.2), *Eupleres* (1539 a), *Rhynchogale* (9.11.25.1) and *Dologale* (9.5.12.3), but it was not seen in *Mungos*, *Bdeogale*, *Crossarchus*, *Ichneumia* etc. Among Viverridae it was seen in *Viverricula* (13.1.6.2), *Prionodon* (13.7 11.2), *Foina* (1084 a) and adult and young *Genetta* (8.6.14 7) and (4 4 9 34), but not in *Fossa*, *Cryptoprocta*, *Paradoxurus*, *Cynogale* etc.

In seals Muller (1925) stated quite correctly that septa may be found in the adult, but she believed these septa to be made of the palatine bones, and so to be peculiar secondary specializations. The septa are found in the Otariidea, in several species of *Otaria* (fig. 14), though poorly developed in *O. jubata*, a very large species (Camb. 907 N), in *Arctocephalus hookeri* (Camb. 904 A), and in *Zalophus californicus* (Camb. 905 A, B). They are in fact of the typical presphenoid type already described in rodents and carnivores. The palatine bones as usual guard the naso-pharyngeal passage, and articulate with the presphenoid, but take no part in the formation of the septum itself. Septa are not found in typical seals (*Phoca*, *Lobodon*, *Cystophora*) or in the walrus (*Trichechus*). In these animals the space between the orbits is occupied, not as in typical rodents and carnivores, by the posterior extensions of the nasal cavities, but by the nasopharyngeal duct which lies just ventral to the cranial cavity.

Primates.

The interorbital septum has not been found in the adult tupaiids or lemurs, but is well developed in most typical primates, including *Tarsius* and New and Old World monkeys, though it is lost in the anthropoid apes and man. In *Tarsius* the orbits are enormous, and in some individuals even encroach on the roots of the molar teeth, which appear as truncated stumps exposed in the orbital floor, cut off flush with the bone (figs. 15 and 16). This feature has been seen also in some individuals of *Herpestes*. The interorbital septum in *Tarsius* is, as would be expected, very large.

When the skull is held up to the light frontal and presphenoidal fenestrae, of about equal size, light up, while between the illuminated areas a more opaque band follows the fronto-presphenoid suture.

A skull broken along the horizontal plane shows the septum in section as a thin sheet of compact bone separating the orbits (fig. 16). The septum passes from the cranio-nasal passage anteriorly to a slightly thickened posterior margin, which contains some cancellous bone and serves as the common anterior boundary to the two optic foramina. This septum is the largest known, relatively to the size of the skull, in any animal. Woollard's (1925) monograph agrees well with the above as far as the individual bones are concerned but there are no detailed descriptions or figures of the region showing the sutures.

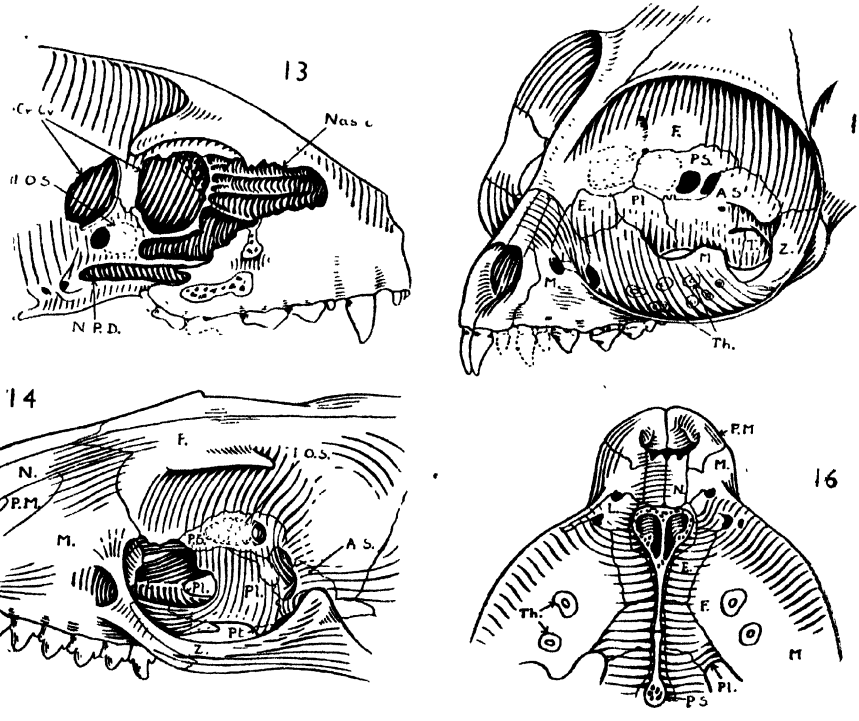
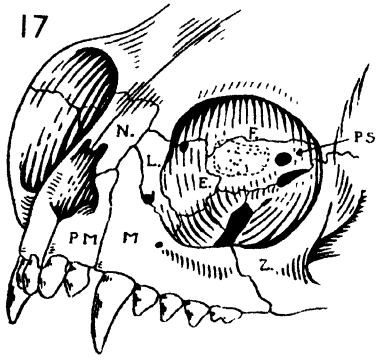


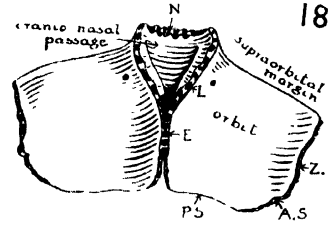
FIG. 13. —*Cynictis penicillata* (B.M. 25.1.2.53), broken skull.
FIG. 14. —*Otaria cinerea* (Camb. 911), dry skull.
FIG. 15. *Tarsius spectrum* (B.M. 90.7.25.1), dry skull.
FIG. 16. —*Tarsius spectrum* (B.M. 46.1.29.2), broken skull.

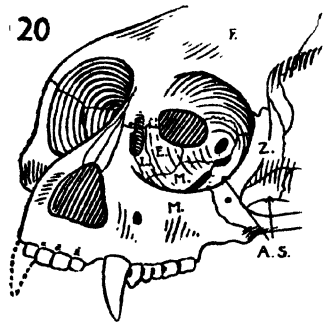
The common marmoset, *Callithrix jacchus*, shows some variability in the constitution of the septum. The posterior part is formed of the presphenoid, and the septum may have only a small extension onto the frontals (fig. 17), or the frontal may take a more important part (fig. 18), or finally a small additional portion may be formed of the ethmoid (Camb. E. 7901 E). Beattie (1927) described the presphenoidal part of the septum accurately (p. 611), but his fig. 11, of a parasagittal section of the skull, shows a large area which must be an interorbital septum, with a vertical suture crossing it. If the suture is correctly drawn the anterior bone must be the frontal, not the ethmoid as it is labelled in Beattie's figure, for the ethmoid is not found in the antero-superior part of the septum in this or any other mammal. His beautiful drawing (his fig. 9) of the skull base shows the optic foramina very close together, as in the rabbit.

Other members of the genus *Callithrix* and other genera of marmosets agree with the common form. A section of the skull of *Mystax* (fig. 19) shows a septum composed of presphenoid, frontal and ethmoid in that order of importance and the septum is seen to have its usual mammalian relationships to the cranial cavity, respiratory apparatus and optic foramina. But since, as in most primates, ethmo-turbinals III and IV have been lost, it is II that lies nearest the margin of the septum.

The squirrel monkeys, *Saimiri* (*Chrysothrix*) have the septum replaced by a large foramen leading directly, in the dry skull, from one orbit to the other (fig. 20). The foramen, filled in life by a membrane, is bounded by rounded borders of the







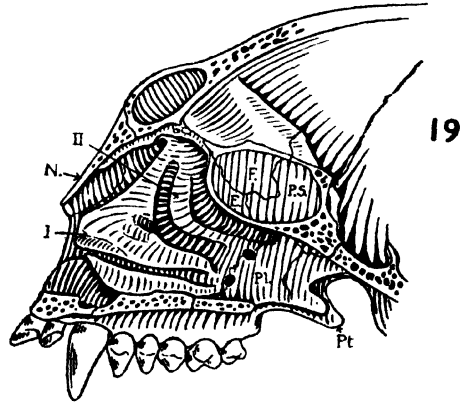


FIG. 17. *Callithrix jacchus* (B.M. 3.10.1.1.), dry skull.
FIG. 18.—*Callithrix jacchus* (Camb. E. 7901D), disarticulated skull.
FIG. 19. —*Mystax rufiventer* (B.M. 3.4.5.3), sectioned skull.
FIG. 20. —*Saimiri sciurea* (B.M. 23.8.10.5), dry skull.

frontal above and the presphenoid and ethmoid below. It is mentioned by Elliott (1914) as a generic peculiarity, and noted independently by Muller (1925), but does not seem to have been figured hitherto. No other mammal has a foramen of this size, but a morphological prototype may be found in *Cercopithecus mona* (fig. 31).

Septa are not developed in all New World monkeys. In *Alouatta* (*Mycetes*) Fischer (1903) noted the absence of a septum, and the optic foramina are widely spaced and separated by a chiasmatic sulcus (fig. 21). Now, in *Sciurus*, taken as a typical mammal without a septum, it was found that the optic nerves diverged round the posterior extensions of the nasal capsules, which enclosed the ethmo-turbinals

IV (fig. 6). But in primates these turbinals and the spaces that contained them have been lost, so that the relationships of the chiasma must be different.

The fine skull of *Alouatta* from Cambridge (fig. 22) shows that the space in the presphenoid was taken up by an accessory air sinus. This sinus was known to Zuckerkandl (1887, p. 66), who considered it, from its position, as a sphenoidal sinus comparable to that of man. He noticed, however, that it could be followed anteriorly into the ethmoidal region, and suggested that it had become secondarily confluent with ethmoidal cells. True ethmoidal cells are now known, however, to be confined among living primates to the African anthropoid apes and man (Cave and Haines, 1940), and apart from pathological conditions involving breakdown

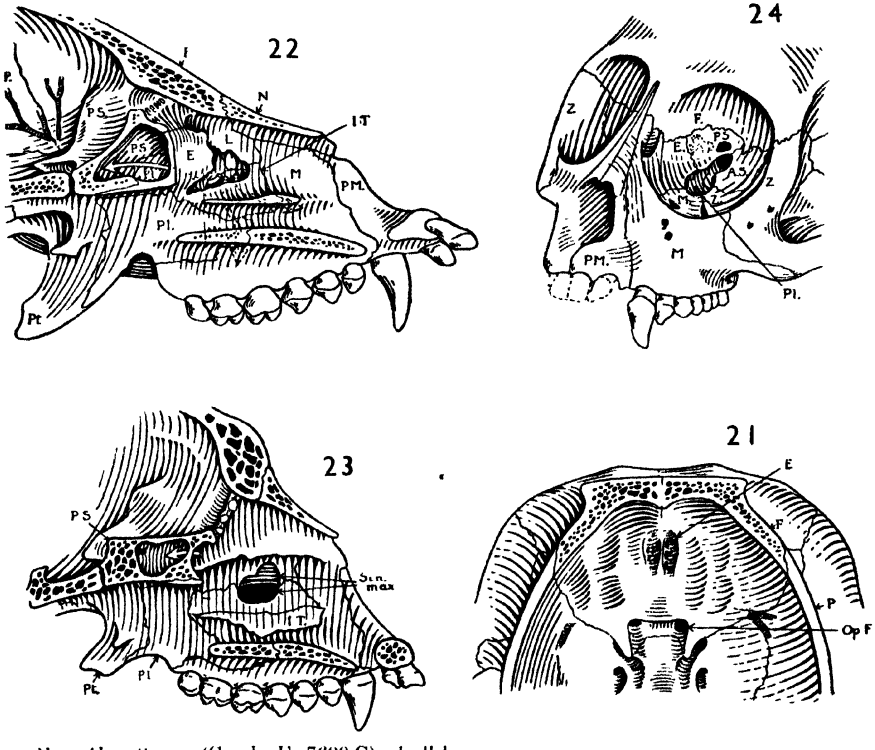


FIG. 21. – *Alouatta* sp. (Camb. E. 7600 C), skull base.
FIG. 22.—*Alouatta* sp. (Camb. E. 7600 C), sectioned skull. Arrows in maxillary sinus.
FIG. 23.—*Brachyteles hypoxanthus* (B.M. 52.12.9.7), sectioned skull. Arrow in sphenoidal sinus.
FIG. 24.—*Cebus* sp. (Camb. E. 7670 D), dry skull.

of the sinus walls the air spaces do not communicate with each other. Further, the space in question has no opening into the back of the nasal cavity, so that it cannot be a sphenoidal sinus.

In fact the space in the sphenoid opens into the side wall of the nasal cavity, in the middle meatus, so that it turns out to be, at least in this individual, a sphenoidal recess of the maxillary sinus, which besides occupying its ordinary position has this posterior extension. A precisely similar condition is found in the orang (Cave and Haines, 1940).

A true sphenoidal sinus does occur in *Brachyteles* (fig. 23). Here again there is no interorbital septum, and as in *Alouatta* the optic foramina are set wide apart, but

the body of the presphenoid is occupied, apart from cancellous tissue, by a sphenoidal sinus whose narrow opening leads directly into the nasal cavity behind the cribriform plate. Cavities such as this must be evolved independently from those in the African anthropoids and man, since their occurrence is sporadic in the New World monkeys and they are not found in the Old World types, yet morphologically they are indistinguishable from those of man.

The capuchin monkeys, *Cebus*, are variable in structure. In Seydel's (1891) *C. hypoleucus* a pair of well developed sinuses occupied the interorbital region, and Paulli (1900) has given an exact description of sphenoidal sinuses similar to that shown in fig. 23. A *C. macrocephalus* (B.M. 1022 a) confirms these descriptions for the bone is broken away on one side exposing a typical sphenoidal sinus opening

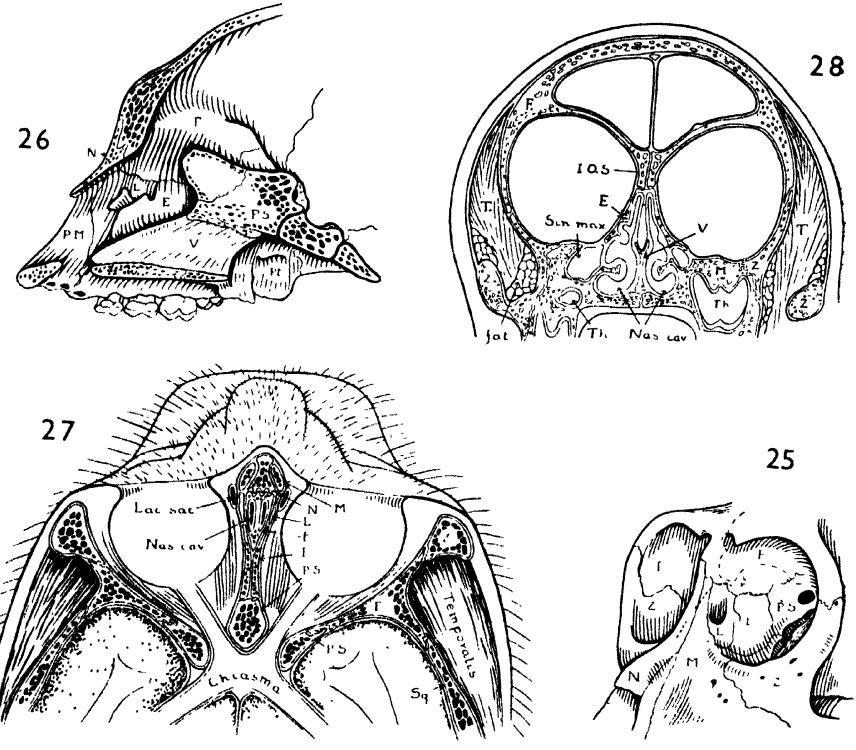


FIG. 25.—*Macacus* sp. (Thos.), dry skull.
FIG. 26.—*Macacus* sp. (Thos.), section of skull
FIG. 27.—*Macacus rhesus*, decalcified head, horizontal section.
FIG. 28. —*Macacus rhesus*, decalcified head, coronal section.

directly into the nasal cavity. But Fischer (1903, p. 401) found septa in adult specimens of *Cebus*, and fig. 24 shows a *Cebus* in which there is no sphenoidal sinus, while a typical, though small, septum is developed in the presphenoid.

The presence or absence of the septum is not associated with any particular species. Among the skulls in the British Museum the septum may be present or absent in *C. albifrons* (50.11.22.23 and 3.9.1.5), in *C. pallidus* (44.8.24.7 and 46.8.24.8), and *C. hypoleucus* (3.3.1.1 3 and 2.3.5.14), and it may be well developed in *C. fatuellus* (90.2.22.3), a species in which Henckel (1928) failed to find it in the embryo. This last record, though based on a single observation, has found its way into the literature as typical of the genus.

In other genera examined, including *Ateles, Nyctipithecus, Aotus, Pithecia*, etc. the septum was always present.

Macacus is the best known genus of the catarrhines, and shows a typical interorbital septum, formed of the presphenoid and the frontal bones, with the frontal component relatively large (figs. 25 and 26). A section of a decalcified head in the plane of the chiasma (fig. 27) shows the septum formed of the single presphenoid posteriorly, and the paired orbital plates of the frontals anteriorly, both containing some cancellous tissue, but this is not too thick for translucency in the dry skull. The relationships of the septum to the optic foramina and the chiasma are just as in the rabbit (cp. fig. 3), for in both animals the septum forms the common anterior margin of the two optic foramina. Anteriorly the relationships are rather different, for owing to the reduction of the nasal cavities and the flexion of the basicranial axis only the extreme upper parts of the cavities, empty of turbinals, appear in the section.

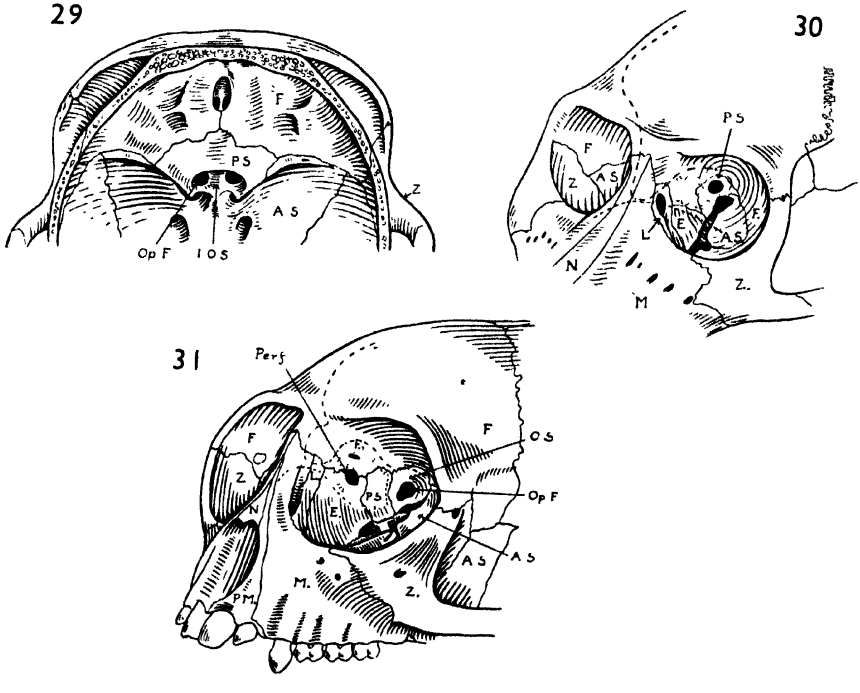


FIG. 29.—*Macacus* sp. (Thos.), skull base.
FIG. 30.—*Papio* sp. (Thos.), dry skull.
FIG. 31.—*Cercopithecus mona* (Zool. Soc.), dry skull.

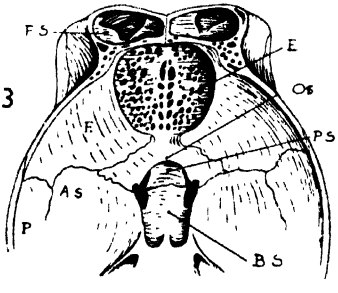
A coronal section through another head (fig. 28) shows the frontal part of the septum between the cranial cavity above and the nasal cavities below. In *Macacus*, as in most monkeys, the extent of the nasal cavities corresponds closely to that of the ethmoid bone, which is ossified in the cartilaginous nasal capsules, so that the lower margin of the septum follows the fronto-ethmoid suture. This is, however, not constant, for both in New World and in Old World forms (figs. 19 and 31) the ethmoid may enter the septum, though the frontal never encroaches on the nasal cavities in these groups.

The skull base (fig. 29) shows the narrow interorbital septum between the optic foramina as in the rabbit (cp. fig. 5). With the reduction of the olfactory apparatus

the cribriform plate has been reduced to a simple cranio-nasal passage, occupying a small field between the orbital plates of the frontal which are expanded to support the frontal lobes of the brain. The territory between the optic foramina and the cranio-nasal passages is formed by the bones that contribute to the septum, the presphenoid and the conjoined frontals.

Other Old World monkeys agree with *Macacus*. *Papio* (fig. 30), for instance, shows the septum with its characteristically large frontal component. Most species of *Cercopithecus* have the same type of septum, but in *C. mona* (fig. 31) the ethmoid takes part in the large septum, and between the frontal and ethmoid there is usually a foramen connecting the two orbits, resembling that already described in *Saimiri* (foramen absent in B.M. 30.11.11.60). The foramen has not been found in other species of the genus with the exception of *C. grayi* (B.M. 0.2.5.4), nor in other genera of Old World monkeys. The skull base of *C. aethiops*, figured by Wood Jones (1929) resembles that of *Macacus*, but the interfrontal articulation is more elongated. The septum itself may occasionally be absent as an individual variation, for Fischer (1903) found it so in a *Macacus*, and it is also absent in *Nasalis larvatus* (Camb. E. 7821 A and C). Unfortunately no cut or broken skull of this species has come to hand, so it has been impossible to discover whether an accessory air sinus has inflated the presphenoid.

There are no interorbital septa in the anthropoid apes, for the sphenoidal body is always occupied by an air sinus. This sinus, just as in the New World monkeys, may be of two kinds, a true sphenoidal sinus as in the gibbons, chimpanzee and gorilla, or an extension of the maxillary sinus as in the orang (Cave and Haines, 1940). In man the sinus is usually the sphenoidal, but occasionally a posterior ethmoidal cell may invade the sphenoid and take its place to a greater or lesser degree.



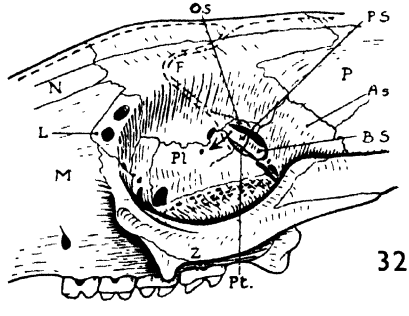


FIG. 32.—*Macropus giganteus* (Bulgakow), dry skull.
FIG. 33.—*Macropus giganteus* (Bulgakow), skull base.

GROUPS WHERE INTERORBITAL SEPTUM IS ABSENT IN THE ADULT.

The interorbital septum has not been found in the adult in monotremes, marsupials, edentates, insectivores, bats, *Galeopithecus*, tupaioids or lemurs. In *Macropus*, for example (fig. 32), the 'posterior root' of the lesser wing of the sphenoid is not developed, so that the optic foramen and superior orbital fissure are confluent. But the anterior boundary of the common opening is formed as usual, below by the presphenoid, which is broad from side to side but shallow vertically, and anteriorly and above by its lesser wing. As the optic nerve emerges (the course is marked in fig. 32 by an arrow) it is separated from the posterior recess of the nasal cavity, which contains the last ethmo-turbinal, by the orbital surface of the frontal bone, and from the capacious naso-pharyngeal duct by the orbital plate of the palatine. The skull base (fig. 33) shows the wide presphenoid articulating behind with the basi-sphenoid and joined anteriorly to the ethmoid. The lesser wings form between them a prominent shelf which overhangs the deep chiasmatic sulcus (between the markers 'P.S.' and 'O.S.').

Interorbital Septum in the Chondrocranium.

In contrast to the septum of adult animals, that of embryos has been discussed exhaustively by a number of authors, particularly Matthes (1922), de Beer and Woodger (1930) and de Beer (1937). In the present survey there will be no need to repeat this work, and precise references will only be given where there is some special reason for doing so.

In all mammals the anterior end of the central stem of the chondrocranium is laterally compressed so as to form the nasal septum. In some embryos the compression stops at the level of the posterior cupulae of the nasal capsules, in which case there is no interorbital septum (figs. 34 A and C, and 36 A), but in other embryos the compression is continued posteriorly into the orbital region, and in this case an interorbital septum is said to be present (figs. 34 B and F, and 36 B). This definition

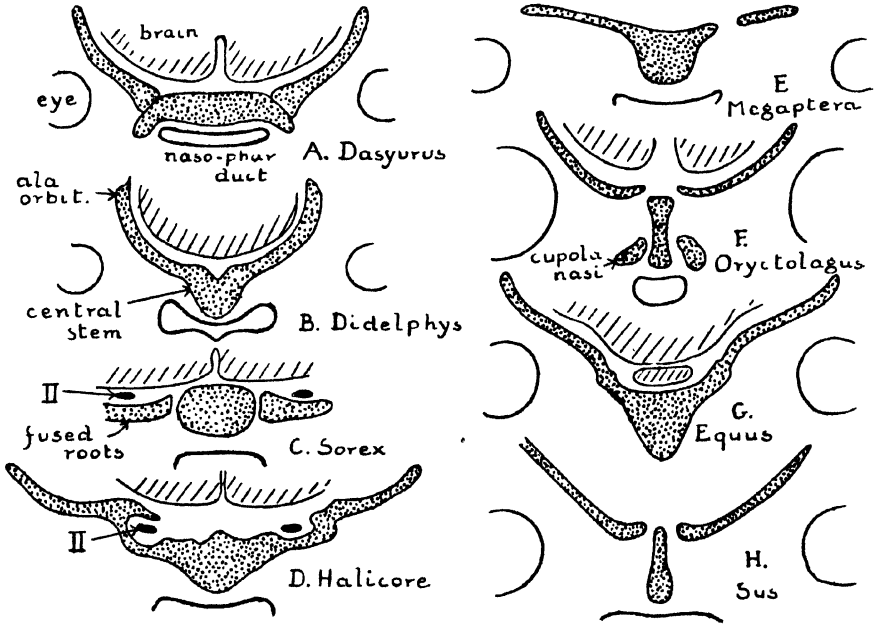


Fig. 34.—Chondrocrania of mammals, transverse sections through orbital region.

A. *Dasyurus* (Broom, 1909).
B. *Didelphys* (Toeplitz, 1920).
C. *Sorex* (de Beer, 1937).
D. *Halicore* (Matthes, 1921).
E. *Megaptera* (Honigman, 1917).
F. *Oryctolagus* (Voit, 1909).
G. *Equus* (Limberger, 1926).
H. *Sus* (Mead, 1909).

agrees with that of Matthes (1922, p. 159), who understood by a typical septum 'eine senkrecht gestellte, mehr hohe als breite, unpaare Knorpelplatte, die als freies Schaltstück zwischen hinterer Nasenkapsel und Pars chiasmatica der Orbitotemporal region (characterisiert durch Ansatz des Orbitalflügels) steht'. The emphasis on lateral compression is important, for writers on the region have not always followed the same procedure in their descriptions, and this has led to difficulties in understanding their work.

Septa are more frequent in embryos than in adults. In monotremes they are found in *Ornithorhynchus*, but not in *Echidna*, and in marsupials in *Didelphys* (fig. 34 B) and *Perameles* (Cords, 1914, p. 49), but not in *Caluromys*, *Dasyurus* (fig. 34 A) or *Trichosurus*. They are not found in any typical insectivores or chrysochlorids

(Roux, 1947), of which *Erinaceus*, *Talpa*, *Sorex* (fig. 34 C), *Suncus*, *Elephantulus*, *Setifer*, *Eremitalpa* and *Chrysochloris* have been described, in the bat *Miniopterus* or in *Galeopithecus*.

In edentates Fawcett's (1921) 12 mm. *Tatusia* has a distinct keel on the under surface of the central stem opposite the preoptic roots, though the formation has disappeared in his 17 mm. embryo, and Weber's (1927) figure of *Bradypus* has the septum labelled, but in neither case are sections given, so that the presence of a septum is uncertain. The sirenian *Halicore* (Matthes, 1921) has a wide, low keel (fig. 34 D), but no definite septum, and it is absent, too, in *Manatus* (Hirschfelder, 1936). In the whales, *Lagenorhynchus*, *Balaenoptera*, *Phocaena* and *Megaptera* (fig. 34 E), the central stem may be keeled to support the rostrum, but there is no true septum, though de Beer and Woodger (1930) give it as 'feebly represented'.

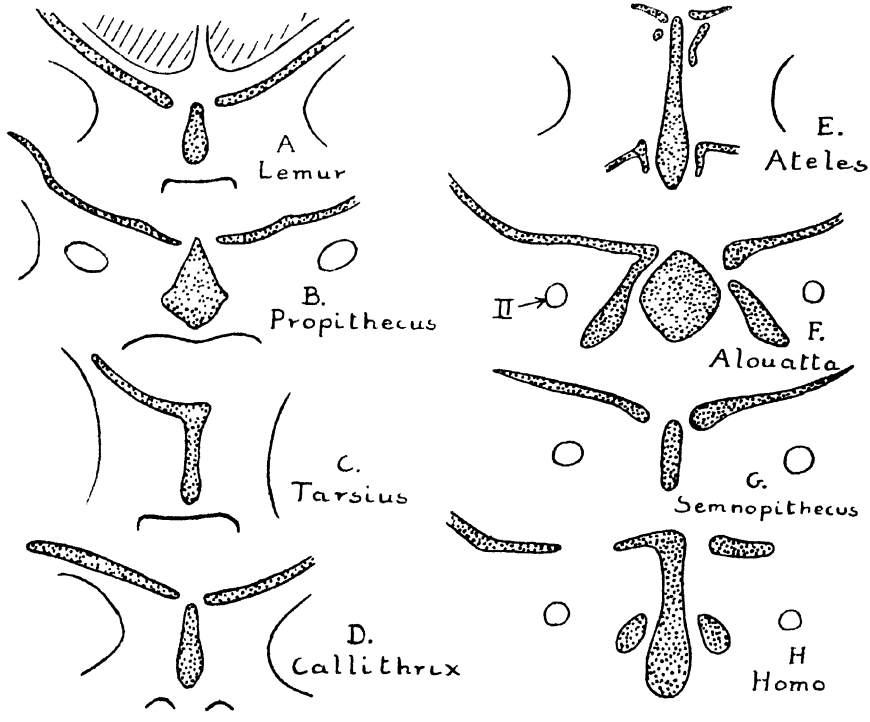


FIG. 35.—Chondrocrania of lemurs and primates, transverse sections through orbital region.

A. *Lemur* (Henckel, 1928).
B. *Propithecus* (Frets, 1914).
C. *Tarsius* (Frets, 1914).
D. *Callithrix* (Henckel, 1928).
E. *Ateles* (Frets, 1913).
F. *Alouatta* (Frets, 1913).
G. *Semnopithecus* (Frets, 1914).
H. *Homo* (Frets, 1914).

In carnivores de Beer and Woodger give the septum as absent in *Felis*, but Terry (1917, p. 318) describes the stem as becoming 'thickened opposite the optic foramina and finally triangular in its most anterior part. Here the two extracranial surfaces incline medially and ventrally to meet in a keel, forming a short interorbital septum which passes forward into the septum nasi'.

In *Canis* de Beer and Woodger give the septum as 'feebly represented', but it is as wide as it is high (Olmstead, 1911). Presumably the septum would be found in the embryos of *Herpestes* and other forms in which it is present in the adult, for though the embryonic septum may be lost in the adult, the reverse is unknown.

In the seal *Poikilophoca* de Beer cites the septum as ' absent ', but Fawcett (1918, p. 417) describes an ' interorbital septum ' which ' somewhat triangular in coronal section behind, changes anteriorly to a pear-shaped outline with the large end downwards '. Indeed, such septa might be expected in the embryos of typical seals, since they are found in the adults of the eared types.

In rodents septa have been found in all three genera examined, *Oryctolagus* (fig. 34 F), *Xerus* and *Arvicola* (*Microtus*), though in the last two they are lost in the adult. In the ungulates the septum is found in *Bos*, also quite definitely in *Equus* (fig. 34 G), though de Beer and Woodger give it as ' absent '. The chondrocranium of *Ovis* has not been sectioned, but Decker (1883) figures a definite septum. Mead's paper on *Sus* has often been overlooked, but his description (p. 193) is definite. ' The basal portion of the regio orbitotemporalis, which lies in front of the sella turcica, is higher than wide and so forms a vertical plate, a true interorbital septum. Near its anterior end, where it joins the nasal septum, it is $2\frac{1}{2}$ times as high as broad '. His figure, too (fig. 34 H in this paper), shows the septum better developed than in any embryo known outside the primates. The chondrocrania of the smaller deer and antelopes have not been examined, but there can be no doubt that such a form as *Neotragus* would show a good septum, for the presphenoid is ossified in cartilage, and indeed some of the cartilage still persists in the adult at the lower margin of the septum (fig. 9). In the hyracoid *Procavia*, also, a short interorbital septum is present in the embryo (Lindahl, 1948). Taking the embryonic and adult structure together, the ungulates must be admitted to a place among the groups in which the septum may be well developed.

Among tupaiids the septum is shown distinctly in the embryo *Tupaia* by Henckel (1928), though de Beer and Woodger (1930) give it as ' absent ' ; it has also been found in all the embryos of lemurs examined, *Lemur* (fig. 35 A), *Nycticebus* and *Propithecus* (fig. 35 B). The septum is large in *Tarsius* (fig. 35 C) and in the New World monkeys *Callithrix* (fig. 35 D), *Chrysothrix* and *Ateles* (fig. 35 E). It is absent in *Alouatta* (fig. 35 F), for the central stem is wide in preparation for pneumatization. It has also been recorded as absent in *Cebus* (Henckel, 1928), but here, as it is variable in the adult, it is probably so in the embryo, and Frets's (1913) most posterior section shows a deep septum persisting in the region of transition between the nasal and interorbital regions. In Old World monkeys the septum is found in *Macacus*, *Semnopithecus* (fig. 35 G) and *Nasalis* embryos. In *Homo* it appears in the embryo as a thin sheet in the early stages (fig. 35 H), but later it becomes thickened (Jacobson, 1928) and finally pneumatized.

Factors Influencing the Presence of the Septum.

Taking the mammals as a whole the interorbital septum is more likely to be developed in animals with large eyes rather than small eyes (ungulates and primates versus insectivores and bats), in young animals rather than old (*Ornithorhynchus* and *Didelphis* embryos versus adults), in small animals rather than large (*Cephalophorus coeruleus* and *Herpestes griseus* versus *C. harveyi* and *H. brachyurus*), in animals with long narrow skulls rather than short broad skulls (*Rhinosciurus* and *Poiana* versus *Sciurus* and *Cryptoprocta*), in animals with the nasal apparatus poorly developed rather than well developed (eared seals and primates versus typical carnivores and lemurs), and in animals with simple nasal cavities rather than those provided with accessory air sinuses (*Madoqua*, *Saimiri* and *Macacus* versus *Ovis*, *Alouatta* and *Homo*).

All these factors influence the width of the orbit relatively to that of the skull in the orbital region, and make it more likely that the orbits will become contiguous so that they are separated by a thin septum only. The eyes and their accessory apparatus do not necessarily fill the orbit, for much of the space may be occupied by fat, but large eyes necessarily imply large orbits to accommodate them. The eyes show pronounced disharmony in growth, for they are relatively much larger in the embryo and young than in the adult, and even though they usually bulge from the

head in the embryo the orbits are relatively larger. In any series of closely-related animals, though the eyes will be found to be larger in the larger types, they do not increase in size proportionately to the other parts (Ashley Montagu, 1944), so that in the smaller members of the series they are disproportionately large. The orbits must remain more or less spherical in shape even when the skull as a whole elongates, so that when this happens the orbits become relatively larger as the skull narrows down. Withdrawal of the nasal apparatus in animals which have become microsmatic, whether through marine or through arboreal life, is likely to bring the orbits into contiguity. Development of air sinuses in the presphenoid may, on the other hand, be secondary to loss of the septum, for they are found only in large animals whose orbits have become separated.

Morphology.

The condition of the interorbital region of the anterior brain-case in non-mammalian tetrapods has recently been reviewed by Save-Sodebergh (1947) and Bellairs (1949). In most modern reptiles a well developed cartilaginous interorbital septum is present in both the embryonic and adult conditions, in snakes and amphisbaenids, however, the septum appears to have been secondarily lost. There is some evidence that a cartilaginous or partly ossified septum was present in cotylosaurs, and that this structure became more extensively ossified in the pelycosaurs and therapsids (Romer and Price, 1940; Olson, 1944). These findings relate to the adult anatomy, but it may be assumed that, as in *Sphenodon*, lizards and crocodiles, an unossified septum was also present in the embryos of these extinct forms.

Conditions in the earliest mammals are not known but the osteology of many Paleocene forms has been worked out in some detail (Matthew, 1937), and no occurrence of a septum has been reported. This negative evidence, together with the fact that the interorbital septum is absent in the adults of the most primitive living mammals (monotremes, marsupials, insectivores) strongly suggests that its presence in more advanced forms is secondary.

The septum of the typical reptilian chondrocranium is, like that of mammals, continuous anteriorly with the nasal septum, and extends back to form the common anterior boundary of the optic foramina. Its upper border is related on either side to the planum supraseptale of the orbital cartilage. This cartilage, which is chondrified from an independent centre in the mesenchymatous brain capsule, is at first separated from the septum by an unchondrified cleft, but later in development fuses with it, and, at least in some forms, contributes tissue to it. Anteriorly the septum is separated from the spheno-ethmoidal commissure, by the orbito-nasal fissure. Below, since there is no naso-pharyngeal duct, the septum abuts freely against the mucous membrane of the mouth. In many forms one or more fenestrae are developed in the septum as development proceeds, but these are secondary deficiencies filled in by membrane, which takes the place of the resorbed cartilage (Bellairs, 1949). In mammals with septate chondrocrania (fig. 36 B, 38 D) the general relationships are maintained, but there are great changes in proportions. The planum supraseptale forms the ala orbitalis, and is still attached to the nasal capsule by a spheno-ethmoidal commissure. But the capsule itself is greatly expanded to include the new ethmo-turbinal apparatus of the nasal cavities. The orbital region of the chondrocranium, with its septum, is shortened, so that the optic foramina and orbito-nasal fissure come near together, narrowing down the originally extensive attachment of the supra-septal cartilage to the septum in reptiles to give the relatively narrow 'pre-optic root' of mammals.

Fischer (1901) and others have suggested that the lateral walls of the nasal capsules migrated backwards in mammals so as to include a part of the original interorbital septum within the nasal cavity, leaving less for the interorbital part, and there is some evidence for this view, as the interorbital region of the central stem is reduced in the older, as compared to the younger, chondrocranium of *Talpa*.

But since the lateral wall is attached to the septum behind the cranio-nasal passage for the olfactory nerve, so that the lateral and medial walls would naturally expand together, and since the backward extension of the orbito-nasal fissure suggests compression of the region behind it, it seems more reasonable to postulate a simple expansion of the nose including its septum and a reduction of the orbital region as major changes in mammalian evolution Either view is compatible with the direct derivation of the mammalian from the reptilian septum.

de Beer and Woodger (1930) found that in the rabbit the septum develops from an unpaired trabecular chondrification which appears at the 16 mm. stage (my fig. 37). This cartilage expands to form a vertical sheet at 16·5 mm . and by 19 mm. has formed a well developed septum continuous throughout the nasal and anterior orbital regions. The anterior part of this sheet, that included between the nasal capsules, forms the nasal septum, the more posterior part the interorbital septum. The alae orbitales develop quite independently of the central stem, and are still, at 19 mm., remote from the interorbital septum, so that the optic foramina and orbito-nasal fissures are not yet separated off from each other. But at 19.5 mm. a bar of cartilage,

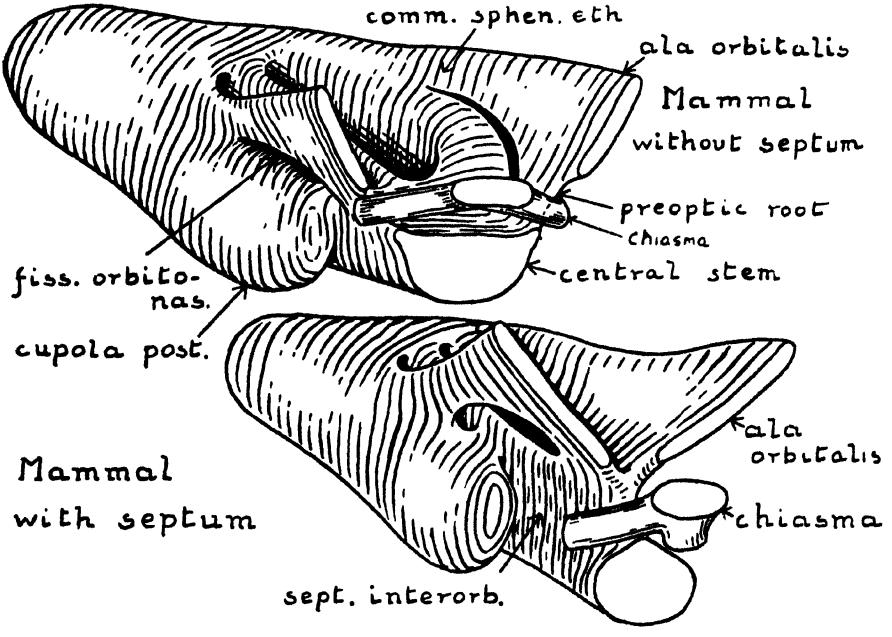


FIG. 36.—Anterior parts of chondrocrania of mammals, without and with septum.

the pre-optic root, joins each ala to the postero-superior corner of the septum. Since by this stage the ala has also become joined to the nasal capsule by the spheno-ethmoidal commissure and to the central stem behind the optic nerve by the post-optic root, the orbito-nasal fissure and the optic foramen are now complete.

In the rabbit, then, the only animal in which the development of the septum has been worked out, it is a direct derivative of the trabecular part of the stem. In the typical reptiles the trabeculae are separate in the precartilaginous stage, a primitive condition no longer found in the rabbit, but the main body of the septum is developed from the fused trabeculae just as in the rabbit (Bellairs, 1949).

Fischer (1903), on finding septa in primate embryos, suggested that the primates had left the primitive mammalian stock at an early stage of their evolution, when that stock still had septate chondrocrania, while the other mammalian groups had progressed to complete obliteration of the septum He did not, at that early date, realize how widespread septa are in mammalian embryos, and other authors have not cared to commit themselves on the question of the primitive state. But taking the evidence of distribution together with that of the close similarity in both the structure and development of the reptilian and mammalian septa, it seems likely that the presence of some remains of the septum in the embryo is a primitive mammalian feature rather than that it has been entirely lost and then regained in a number of mammalian groups. In animals such as *Echidna*, most marsupials, edentates, and insectivores where there is no septum, a series of features, more or less pronounced in any particular instance, is usually found together (fig 36 A).

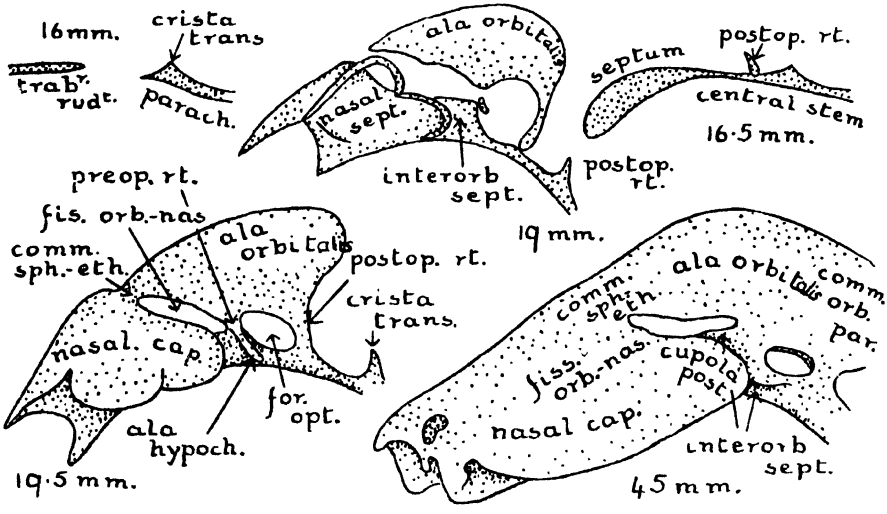


FIG. 37. Development of chondrocranium of rabbit (de Beer and Woodger, 1930; Vort, 1909).

The nasal capsules are large, the orbito-nasal fissure reduced to a narrow cleft or partially obliterated, the central stem wide, the ala orbitalis narrow antero-posteriorly, and the pre- and post-optic roots thin, absent or joined together before they are attached by a common root, so that the optic nerve pierces the ala instead of passing between it and the central stem. All these trends are away from reptilian conditions, so there is no difficulty in considering them as secondary, and the animals in which they are developed as specialized in these respects.

Fischer's (1901) diagram (my fig. 38 A), comparing a lizard and a mole, shows very clearly the expansion of the nasal capsule and brain and the reduction of the orbital region of the central stem between them, with the displacement of the eye on to the side of the nasal capsule, but the mole, with its small, laterally placed eyes, is not a typical mammal. Muller's (1935) diagram (my fig. 38 B) shows the orbits forced apart in the mammal, but suggests little of the anatomical structures involved. The attempt to summarize my conception of the region (fig. 38 C, D) includes the chiasma and optic foramina as relevant details and shows the septum as disappearing rather than as being split open or included in the nasal cavity.

As regards the persistence of the septum in the adult, Voit (1909) and others have already suggested that its presence in the rabbit is correlated with the large size of the eyes, and the sporadic occurrence of the septum in other rodents and carnivores can usually be associated with the delicate visual control of leaping, hunting and other activities. The smaller living ungulates live in the thick undergrowth of forests, and are crepuscular in habit. Their eyes are very large and provided with tapeta, which increase sensitivity at low illuminations at the expense of acuity, and such eyes can only be accommodated in small skulls by bringing the orbits together and so forming an interorbital septum. Since it is reasonable to believe that the ancestral ungulates were small, forest-living animals, it seems probable, that the septa are

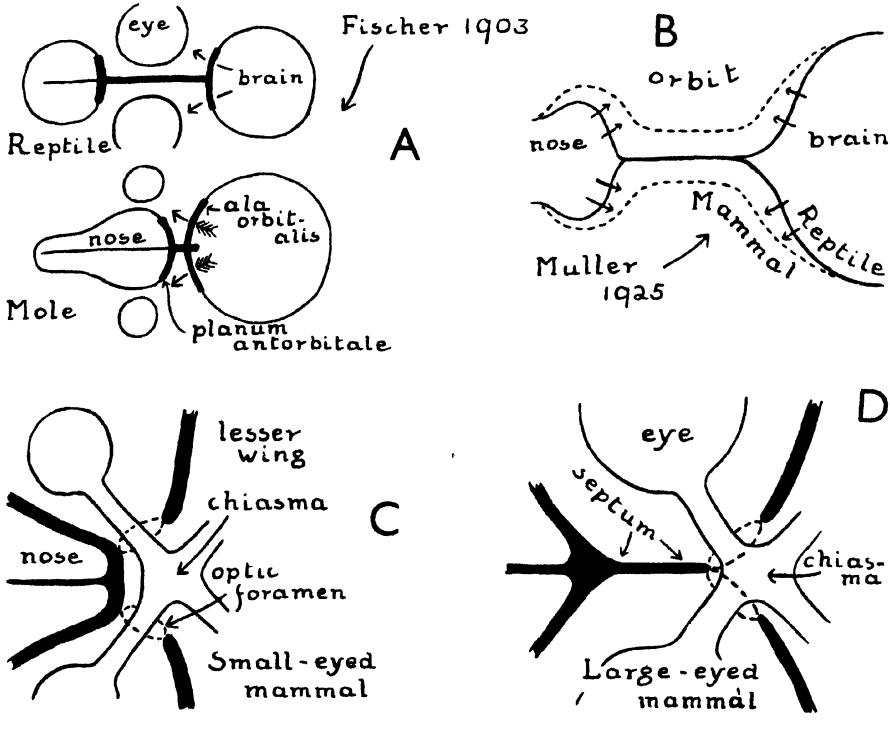


FIG. 38.—Diagrams of chondrocrania. A: Fischer (1901), reptile and mole. B: Muller (1935), reptile and mammal. C, D: Present author, mammal with (D) and without (C) septum.

primitive features of the group. In the larger types the growth of the skull as a whole has separated the orbits, so that though the septa may be well developed in the embryo they are lost in the adult. Further, in late embryonic life, extra ethmoturbinals beyond the ordinary mammalian quota and a complicated system of air sinuses are added to the nasal apparatus (cp. Vogler, 1926, 28 cm. pig embryo, and Zuckerkandl, 1887, adult pig), and these come to occupy the space between the orbits.

In primates all authors are agreed that the septum is a primitive feature. The separation of the orbits in some of the larger forms probably depends partly on the growth of the skull as a whole, and partly on the expansion of the brain.

Floor of the Skull.

The ethmoid, presphenoid and frontal bones all help to build up the floor of the brain case in the orbital region, but their exact arrangement is variable. The ethmoid may articulate with the presphenoid on the surface of the floor, e.g. in *Hemiechinus* (fig. 39) or the frontals may pass behind the ethmoid so as to articulate with each other, cutting off the ethmoid from the presphenoid, e.g. in *Oryctolagus* (fig. 5).

Wood Jones (1929) suggested that the ethmoid-presphenoid contact was typical of mammals in general (e.g. marsupials), whereas the frontal extensions were characteristic of monkeys and anthropoid apes (' with the single variable exception of the orang '), as opposed to man who had retained the primitive contact. So, he argued, man was free from this simian specialization, and could not have been derived from a simian type of ancestor. Ashley Montagu (1930) has criticized the argument, and has recently (1943) published a careful summary of the facts based on an

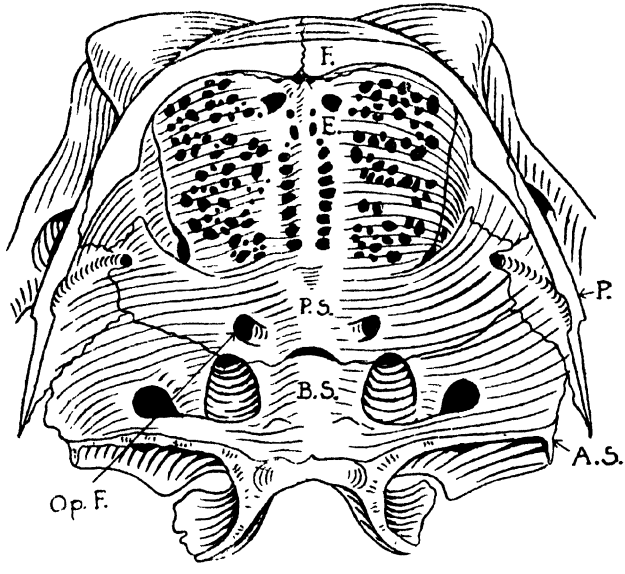


Fig. 39.—*Hemiechinus auritus* (Kamal Wassit), skull base.

adequate series of skulls. It now appears that the anthropoid apes are much more variable than had been supposed, for he found the ethmoid-presphenoid contact in all orangs, most chimpanzees and some gorillas. But neither Ashley Montagu nor any other author has attempted any morphological explanation of these variations.

Now, in marsupials (figs. 32, 33) and insectivores the body of the presphenoid is stout, for it encloses the nasal cavities as they extend back to the region of the optic foramina (cp. Wood Jones's *Dasycercus* and my fig. 6) and in this case it may be widely exposed on the floor of the skull, and the frontals thereby be excluded from contact with each other in this region (fig. 40 A). But where the body of the presphenoid forms a narrow interorbital septum the frontal bones may grow in to articulate with its upper margin, and at the same time with each other, so that the presphenoid is excluded from this part of the floor (fig. 40 B). When the frontal bones themselves help to form the septum then they must necessarily meet in the cranial floor as they turn ventrally into the septum (fig. 40 C).

It has been shown that in most New World and Old World monkeys there is a well developed septum, so that, as would be expected, the frontals separate the ethmoid and presphenoid. Exceptions may be anticipated only in the relatively few forms where the septum has been lost owing to the inflation of the presphenoid by air sinuses, and indeed the only records of ethmoid-presphenoid contacts are in *Alouatta* (Ashley Montagu, 1943), a peculiar form which no morphologist would consider as illustrating primitive conditions. Similarly the presence of the contact in anthropoid apes and man is correlated with the inflation of the presphenoid by highly developed air sinuses, and the condition of the skull base, which is but the surface effect of the underlying structure, must be considered a secondary reversion and not truly primitive. In fact, the evidence of the orbital region can be taken as supporting the close relationship of the anthropoid apes and man rather than the reverse.

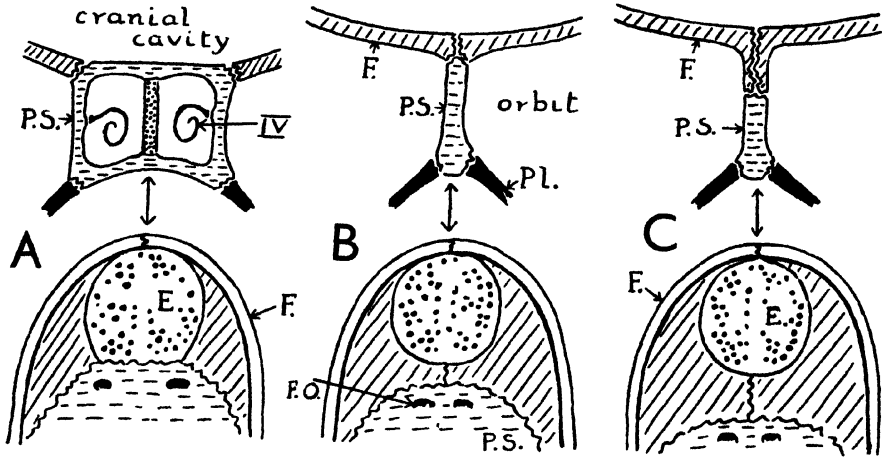


FIG. 40.—Structure of orbital region and skull base.

IRREVERSIBILITY OF EVOLUTION.

The development of the conception of irreversibility of evolution has been carefully reviewed by Petronievics (1919). Dollo's first enunciation, in 1893, 'Un organisme ne peut retourner, même partiellement, à un état antérieur, déjà réalisé dans la série de ancêtres', referred to the organism as a whole, and his later statement of the law merely elaborates his conception. 'Un organisme ne reprend jamais exactement un état antérieur, même s'il se trouve placé dans des Conditions de l'Existence identiques à celles qu'il a traversé. Mais, en vertu de l'Indestructibilité du Passé, il garde toujours quelque trace des étapes intermédiaires qu'il a parcouru'. But Dollo's examples, the pseudo-dentition of an Eocene bird, the pelvis of dinosaurs, the tentacular arms of octopods, etc., refer, not to organisms as a whole but to parts of organisms. The modern conception of reversibility is represented more closely by Arber's (1919 a) 'general rule that a structure or organ once lost in the course of phylogeny can never be regained: if the organism subsequently has occasion to replace it, it cannot be reproduced, but must be constructed afresh in some different mode', though this rule was formulated independently on botanical evidence. Needham (1938) has extended the formulation to include physiological as well as morphological traits, 'Evolution is reversible in that structures or functions once gained may be lost, but irreversible in that structures or functions once lost can never be regained', quoting as examples the enzymes of bacteria, the physiological uraemia of elasmobranchs, the nitrogen metabolism of molluscs, and so forth.

Now, Arber (1919 b) collected together a number of examples of reappearances of lost organs, some of which have been put forward as exceptions to the 'law', including the reappearance of stamens and ovary chambers in plants and of toes in mammals, and Cave and Haines (1944) have added ethmoturbinals in man. But, as Arber pointed out, these organs are all members of series, and their reappearance can be considered as examples of meristic variation.

Reversals of evolutionary trends are generally accepted by palaeontologists, for example the reduction of the lower jaw in the later elephants and the shortening of the legs in forest horses, and Petronievics (1919) suggested that 'if a part degenerates, but if the disposition of the germen is not too enfeebled, it can be followed by a progressive evolution', a view elaborated by Muller (1939). Gregory (1935) quoted several instances from primate evolution where the 'law' of irreversibility had been applied too strictly in ruling out possible phylogenies involving minor reversals of trend. Matthew (1937, p. 321) went further, for he suggested that as regards individual parts complete reversibility was possible, given that they were 'of such simple form that the end results of a re-adaption could not be practically distinguished from the primary adaption', and quoted as examples the tritubercular external form of the teeth in certain seals and whales (cp. my fig. 14).

The interorbital septum is a clear example of Matthew's type of reversibility of simple adaptions. It was developed in the ancestral reptiles, lost in early mammals, redeveloped in typical primates and small ungulates, and lost again in some monkeys, anthropoid apes and man, and in the larger ungulates. It is a simple structure dependent for its existence on the arrangement of other structures in its neighbourhood, its 'germen' is always found in the embryo as a part of the central stem of the chondrocranium, and there is no reason why it should not disappear or reappear in the course of evolution. The ethmoid-presphenoid contact, present in typical mammals and presumably in early types, lost in typical primates, and regained in some monkeys and anthropoids and in man, is another example of the same kind.

Summary.

1. The distribution, relationships and structure of the adult interorbital septum are described and figured in all groups of mammals known to possess it.

2. These include several carnivores and ungulates, besides the eared seals, rodents and primates, where septa were known previously.

3. In primitive mammals septa were not found in the adult skull, but may have occurred in the chondrocranium of the embryo

4. Possession of a septum in the adult is a primitive feature of the ungulates and primates. In both groups the septum may be lost in later evolution

5. The structure of the base of the skull is correlated with that of the septum, for when the frontal bones take part in the septum they must meet each other behind the cribriform plate of the ethmoid.

6. Evolution is reversible in the case of such simple adaptions as the interorbital septum or the ethmoid-presphenoid bony contact.

My thanks are due for the loan of material in the British Museum (B.M.), the Museum of Vertebrate Anatomy, Cambridge (Camb.), St. Thomas's Hospital Medical School (Thos.), the London Zoological Society (Zool. Soc.), the London Hospital and Dr. Kamal Wassif and Dr. Bulgakow of Fouad I University, Abbassia, Cairo.

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EXPLANATION OF LETTERING.

A line of dots and dashes (– · · – · – · – · · – · ·) indicates the extent of the cranial cavity in several of the figures, and a line of dashes (- - - - - - - -) that of the nasal cavity and nasopharyngeal duct. The interorbital septum is stippled.

ala hypoch.	ala hypochiasmatica.	*N.P.D.*	nasopharyngeal duct.
A.S.	alisphenoid.	*nasal sept.*	nasal septum.
B.S.	basisphenoid.	*O.M.*	orbital muscle.
comm. orb. par.	commissura orbito-parietalis.	*O.S.*	orbitosphenoid.
comm. sphen. eth.	commissura spheno-ethmoidalis.	*P.*	parietal bone.
Cr.Cv.	cranial cavity.	*parach.*	parachordal.
crista trans.	crista transversalis.	*preopt. rt.*	preoptic root
cupola post.	posterior cupola.	*postopt. rt.*	postoptic root.
E.	ethmoid bone.	*perf.*	perforation.
F.	frontal bone	*P.M*	premaxilla.
fis. orb. nas., *fiss. orbito-nas.*	orbito-nasal fissure.	*P.S.*	presphenoid.
		Pl.	palatine .
F.O., *for. opt.*	optic foramen.	*Pt*	pterygoid bone or muscle.
F.S.	frontal sinus.	*R.L.*	rectus lateralis muscle.
i.o.s., *interorb. sept.*	interorbital septum.	*R.M.*	rectus medialis muscle.
		Sin. max.	maxillary sinus.
I.P.P.	internal pterygoid plate.	*S.O.*	superior oblique muscle.
I.T.	inferior turbinal.	*Sq.*	squamosal bone.
L.	lacrymal bone.	*T.*	temporal bone or muscle.
Lac. sac.	lacrymal sac.	*Th.*	tooth.
Mas.	masseter muscle.	*Tr. C.*	trabecula cranii.
M.	maxilla.	*trabr. rudt.*	trabecular rudiment.
N.	nasal bone.	*V.*	vomer.
nasal cap.	nasal capsule.	*Z.*	zygomatic bone.
Nas. cav.	nasal cavity.	*I*, *II*, *III*, *IV*.	ethmoturbinals.

The development of the chondrocranium of *Notopterus*.

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(With 12 Text-figures.)

[Read 12 May 1948.]

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1. INTRODUCTION.

The superfamily Mormyroidea, which includes the Mormyridae, Notopteridae and Hyodontidae, forms an interesting group among the clupeiform fishes, and exhibits peculiar specializations in comparison with other Clupeiformes. The chondrocranium of a few Clupeiformes is known, since representatives of some families have been worked out, but very little information exists regarding the embryonic skull of the Mormyroidea. Among this group only that of *Gymnarchus* (Mormyridae) is known to any extent.

The chondrocranium of *Gymnarchus* shows considerable specialization when compared with the embryonic skull of *Salmo*, which may be regarded as representing the generalized type of the Clupeiformes. Since our knowledge of the chondrocranium of the Mormyroidea is very incomplete, there is considerable scope for further additions to it. The following work on the chondrocranium of *Notopterus* was, therefore, undertaken at the suggestion of Professor G. R. de Beer, F.R.S. The chief aim was to find out whether the embryonic skull of *Notopterus* follows the lines of specialization seen in *Gymnarchus* or resembles more the non-specialized *Salmo*.

In this paper a few selected larval stages are considered. The relative age of the different stages is not known; therefore, the length of the larvae is taken as an arbitrary guide. The chondrocranium was studied both by sections and whole transparent mounts prepared by a slight modification of van Wijhe's method, since his original method (1922) did not yield satisfactory results. This was probably because the material is very old (collected in 1915) and perhaps was not fixed in any sublimate fixative. (The fixative used at the time of collection was not recorded.) For the preparation of transparent mounts the larvae were stained in 5% solution of Victoria blue in 70% alcohol for about 12 hours, then differentiated for 2–3 days in neutral 70% alcohol. If sufficient differentiation did not take place during this period, treatment with $\frac{1}{2}$ to 1% acid alcohol was resorted to. After complete dehydration, the stained larvae were passed through up-grading mixtures of absolute alcohol and benzyl benzoate and finally transferred to pure benzyl benzoate, in which they were stored for a number of weeks. The larvae were dissected in this reagent and then after a 3 to 5 minutes' immersion in xylol were mounted in ordinary xylene-balsam in glass cells. Camera lucida drawings of the chondrocranium of dissected larvae were made; in most cases when they were still in the storing fluid. This facilitated proper orientation in any desired position.

The work was carried out in the Department of Embryology, University College London, under the supervision of Professor G. R. de Beer. I am extremely grateful

to him for suggesting the problem, for providing the material, and for his continuous guidance, help and encouragement during the course of the work. I am also grateful to Dr. P. Ford for his friendly help.

2. Description of Specimens.

Stage A. Unhatched embryo 9.5 mm. long.

In this specimen, which is the youngest of the series studied, most of the cartilages of the neurocranium are present and joined up. It is therefore not possible to say anything about their method of origin.

The trabeculae extend well forward in the region of the snout, where they do not join with one another, but each ends freely (fig. 2). Posteriorly each trabecula is fused with the parachordal of its side. Except in the anterior region, where they are comparatively broad, the trabeculae in the remainmg part of their length are cylindrical in section and partly curved in shape: they are widely separated from one another. The parachordals are in the form of broad plates of cartilage on each side of the notochord, which separates them. The pro-otic bridge has not yet formed. Its future position is indicated by two small and broad processes extending from the parachordals towards the median line behind the anterior end of the notochord. Fairly well chondrified auditory capsules are present. Each capsule is fused to the parachordal by means of the anterior and posterior basicapsular commissures. The space surrounded by these two commissures, the lateral

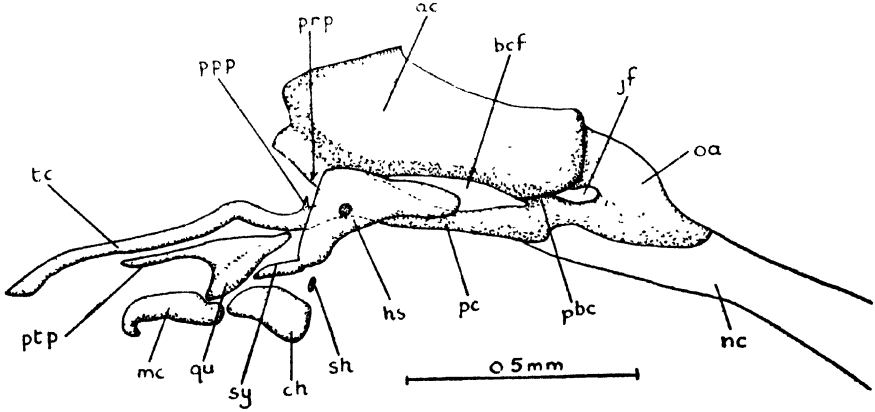

Fig. 1.—*Notopterus chitala*—Stage A, 9·5 mm. long—Lateral view of the chondrocranium.

edge of the parachordal and the medial edge of the floor of the auditory capsule is the basicapsular fenestra. The auditory capsules are at a higher level than the parachordals (fig. 1). From the posterior region of the parachordals arise a pair of occipital arches, separated by the notochord. Each arch is fused with the hind wall of the auditory capsule, leaving a large jugular or metotic foramen for the exit of the vagus nerve.

This embryo is of interest in showing the rudiments of the future lateral commissure: the post-palatine and the pro-otic processes. The former projects latero-dorsally in front of the anterior basicapsular commissure, the latter process, which is smaller and less prominent, projects latero-ventrally from the wall of the auditory capsule.

Fig. 2 shows that the bilateral topographical disposition of the cartilages of the visceral arches is markedly asymmetrical; the neurocranium also shows a twist but to a lesser degree. This is due to the fact that the embryo lies on one side (here

left side) on top of the yolk, more or less compressed between the egg-membrane and the yolk. The developing embryo is thus forced to follow the curvature of the egg. This leads to stretching of the outer side and to compression of the inner side, and results in the topographical displacement of the cartilages of the two sides. This asymmetry is temporary, since at hatching the cartilages become bilaterally symmetrical.

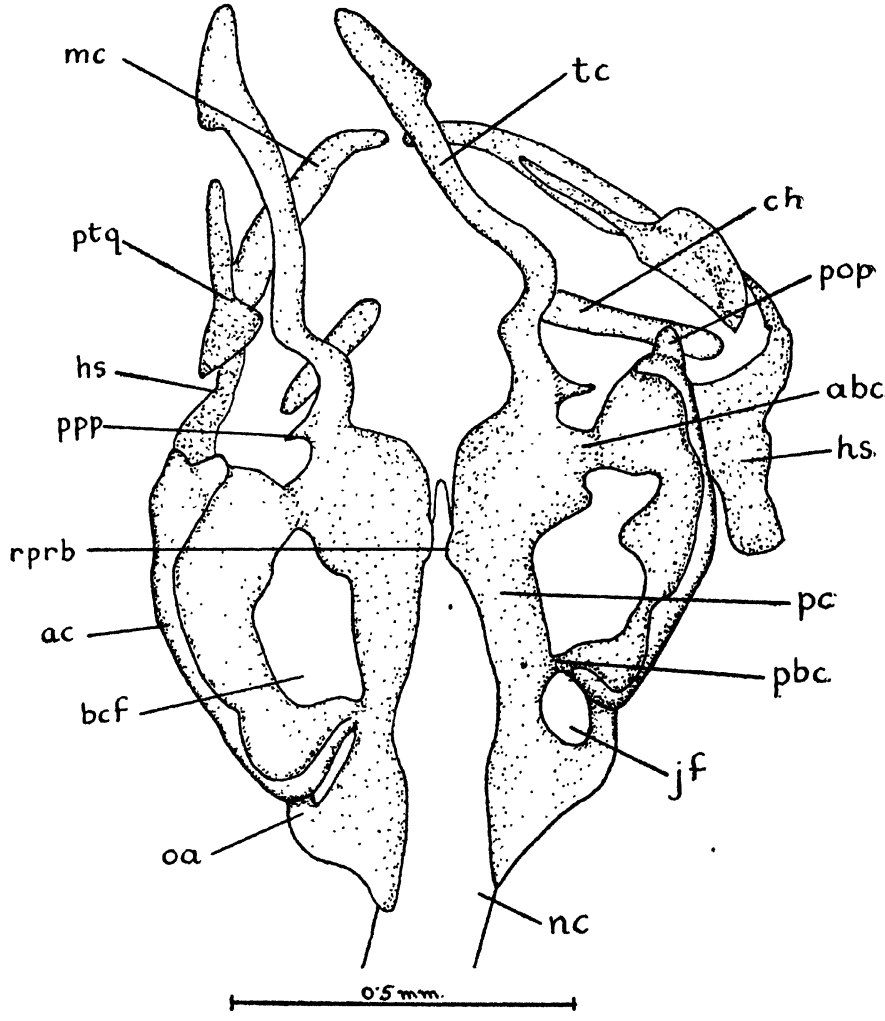

Fig. 2.—*Notopterus chitala*—Stage A, 9·5 mm. long—Dorsal view of the chondrocranium.

In the visceral arches, only the skeleton of the mandibular and hyoid arches is formed (figs. 1 and 2), none of the cartilages of the branchial arches is yet developed. The mandibular arch consists of the pterygoquadrate and Meckel's cartilages. The latter are well developed and do not meet one another anteriorly to form a symphysis. In the pterygoquadrate the quadrate region is made up of thick cartilage, from which the pterygoid process stretches as a thin plate. The pterygoid process ends

approximately half-way along the length of the trabecula. The hyoid arch is represented by the hyosymplectic, interhyal and ceratohyal. Hypo- and basihyals have not yet formed. The head of the symplectic is attached only in the anterior half of its length to the auditory capsule. A marked constriction in the lower part of the hyosymplectic makes the symplectic portion easily recognizable from the rest of the cartilage. The hyosymplectic is pierced by a foramen for the hyomandibular nerve. The ceratohyal is broad and massive.

A small and independent interhyal or stylohyal lies between the ceratohyal and hyosymplectic.

Stage B. Unhatched embryo. 13 *mm. long*

Since this embryo continued to grow while still pressed under the outer egg-membrane, the bilateral asymmetry has become more pronounced.

The anterior ends of the trabeculae have come nearer to each other but are not yet joined. A narrow pro-otic bridge has been established, the cartilage of which passes dorsally to the notochord. The lateral commissure has been completed by the further growth and subsequent fusion of the post-palatine and pro-otic processes (fig. 3).

The pterygoid process has grown further forwards reaching near the broad anterior portion of the trabecula. The head of the hyosymplectic is now attached in its entire length to the auditory capsule. The stylohyal has now established a

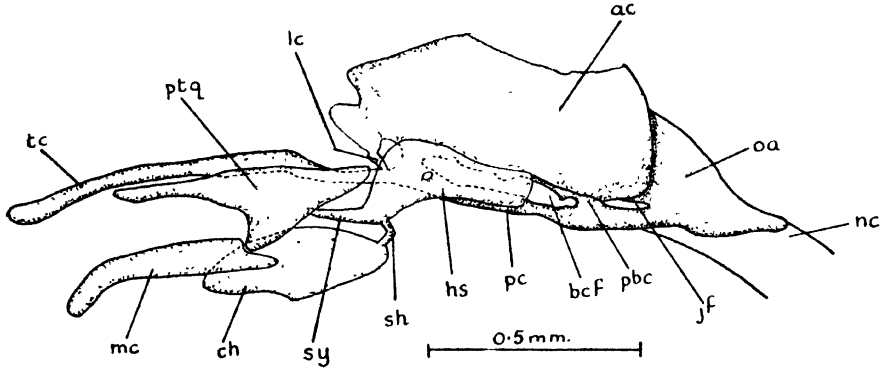

FIG. 3.—*Notopterus chitala*—Stage B, 13 mm. long—Lateral view of the chondrocranium.

cartilaginous fusion at one end with the hyosymplectic and at the other with the ceratohyal. A pair of hypohyals has appeared (fig. 4). The basihyal is not chondrified. In the branchial arches, the first, second and third ceratobranchials and two median copulae, one behind the other, have appeared. The anterior copula is quite short and is situated just behind the hypohyals. The posterior copula is long and constricted approximately half-way along its length. It extends from a short distance behind the anterior copula to a little in front of the second ceratobranchials.

Stage C. In the process of hatching. 14 *mm. long.*

This specimen was evidently fixed when it was in process of hatching. The trunk and tail of the larva have come out of the outer egg-membrane, which has partly broken down, the head is still held (but dorso-ventrally, and not laterally as in the earlier stages) between the membrane and the yolk. The bilateral symmetry is almost restored.

In this stage some new features have appeared. Anteriorly the trabeculae have joined with one another to form the ethmoid plate (fig. 6). The hypophysial fenestra is, therefore, now fully established, bounded laterally by the trabeculae,

anteriorly by the ethmoid plate and posteriorly by the pro-otic bridge. In the anterior region of the ethmoid plate the internasal septum is growing in the form of a small upturned median plate of cartilage (fig. 5). The rudiment of the lamina orbito-nasalis has appeared in the form of a small vertical process growing from the latero-posterior corner of the broad lateral expansions of the trabecula. More dorsally, an isolated triangular plate of cartilage has appeared. That this is the rudiment of the pre-optic root of the orbital cartilage is evident from its relations to nerves and blood-vessels. The post-orbital root of the orbital cartilage is seen growing from the auditory capsule as a post-orbital process. It is pierced by a

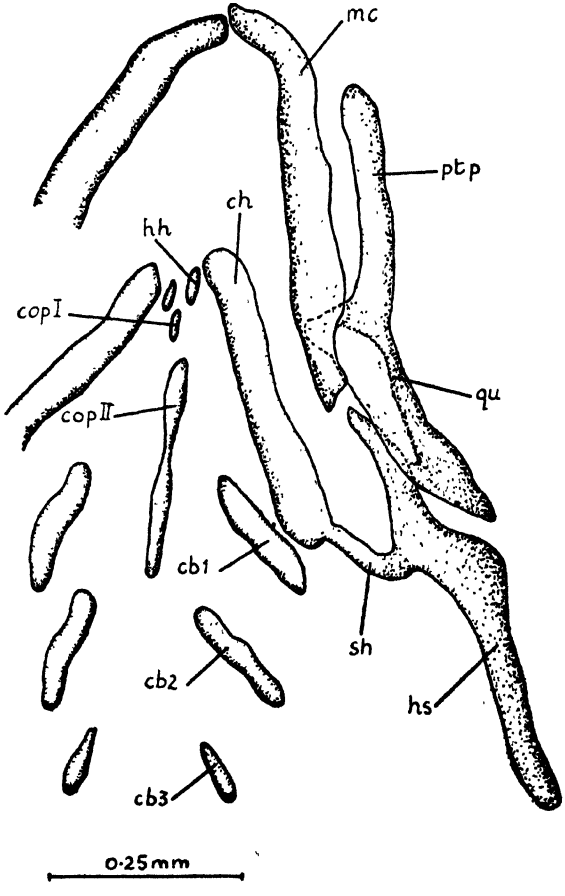

FIG 4 —*Notopterus chitala*—Stage B, 13 mm. long—Ventral view of the visceral arches.

foramen for the otic branch of the facial nerve. Considering the very small size of the otic nerve the foramen is quite large.

The lateral wall of the auditory capsule has grown further upwards. Laterally to the ampulla of the anterior semicircular canal, a hole is created in the lateral wall of the auditory capsule. Evidently this was caused by secondary removal of cartilage, since in earlier stages this area was occupied by cartilage. This hole, however, does not lead to the formation of a fenestra in the skull as it is covered by the intertemporal bone. Inside the auditory capsule three small cartilaginous septa

for the semicircular canals are present. In fig. 5 these septa are drawn as seen through the semi-transparent cartilage of the lateral wall of the capsule. The basicapsular fenestra is considerably reduced and is divided into two portions by the growth of cartilage (fig. 6). The floor of the auditory capsule shows two depressions, one for the utriculus and the other for the sacculus. The floor of the lateral depression, which lodges the utriculus, is at a higher level than that of the other. The posterior wall of the auditory capsule is turned backwards, inwards, and forwards. The anterior edge of the occipital arch is fused to the lateral aspect of the hind wall of the capsule. The foramen for the glossopharyngeal nerve is seen near the posterior end of the longitudinal ridge which marks the lateral boundary of the inner depression of the floor. Behind the pro-otic bridge the parachordals of both sides

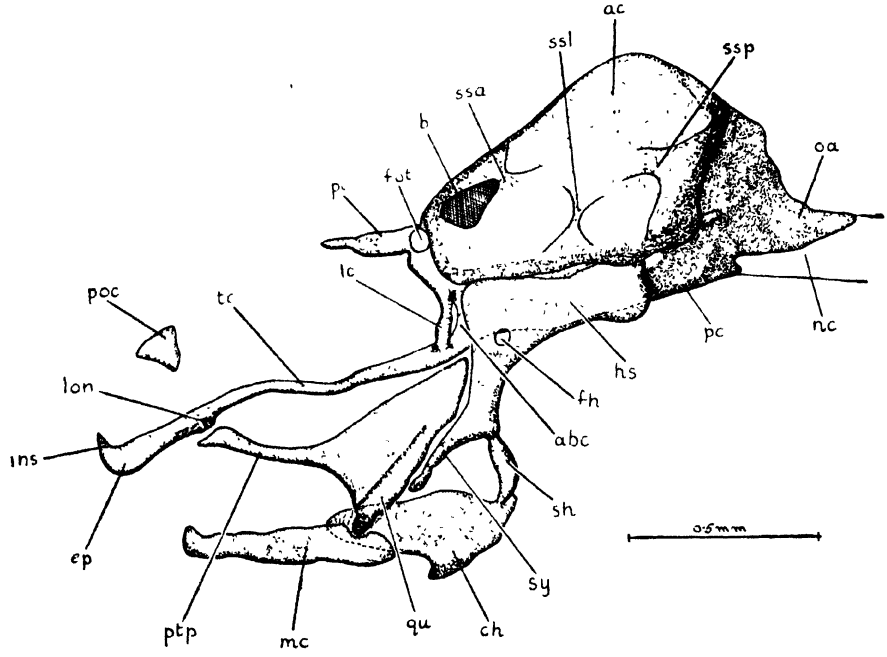

FIG. 5.—*Notopterus chitala*—Stage C, 14 mm. long—Lateral view of the neurocranium and a part of the visceral arches.

are unconnected with one another either below or above the notochord. There is no basicranial fenestra.

The head of the hyosymplectic has grown further backwards. A median basihyal has appeared between the hypophyals (fig. 7). It extends a little distance anteriorly to the hypohyals. The first and second copulae, which chondrified separately in the previous stage, are now fused into a single copula, which extends back to the level of the third ceratobranchials. A ceratobranchial has appeared in the fourth branchial arch. Hypobranchials have appeared in the first and second branchial arches.

Stage D. Hatched larva. 16 *mm. long.*

The pre-optic root has grown downwards, without, however, reaching near the trabecula. The lamina orbito-nasalis has extended upwards in the form of a pillar, the median aspect of which is fused to the lateral surface of the pre-optic root.

Midway along the dorso-anterior margin of the quadrate a small basal process has appeared projecting antero-medially towards the trabecula.

In the visceral skeleton the ceratobranchial has appeared in the fifth branchial arch and epibranchials have appeared in the first four branchial arches. The hypobranchial is now also formed in the third branchial arch. The copula has extended backwards in the region of the fifth branchial arch in the form of median condensations of cartilage (between the fourth and fifth ceratobranchials) interconnected with one another and with the copula of the previous stage by means of procartilage.

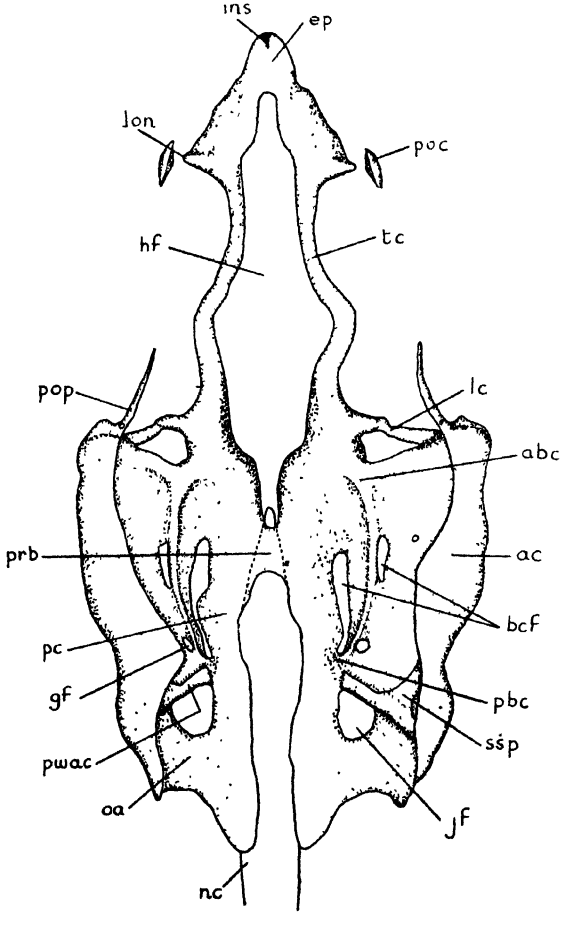

FIG. 6.—*Notopterus chitala*—Stage C, 14 mm. long—Dorsal view of the neurocranium.

Stage E. Hatched larva, 17 mm. long.

The neurocranium does not show any change of importance, except that the internasal septum has extended further upwards, and a narrow tectum synoticum has developed over the auditory capsules.

The basal process has grown considerably in size. There is no indication of a basi-trabecular process.

Pharyngo-branchials have appeared in the first four branchial arches (fig. 8). The first pharyngo-branchial is comparatively small; and the last two are interconnected with one another. The copula has become quite massive.

Stage F. Hatched larvae, 18 mm. long.

The cartilage of the internasal septum is produced upwards in the shape of a pointed dagger (fig. 9). The lower half of the septum is thick, the upper half consists of a thin medial plate of cartilage. The pre-optic root has grown considerably, but it ends ventrally a little distance above the trabecula. Anteriorly the pre-optic root is joined to the posterior median edge of the internasal septum by means of a broad and curved spheno-septal commissure. Posteriorly the pre-optic root is produced into a narrow taenia marginalis, which posteriorly ends freely at a level below the anterior end of the postorbital process.

The lamina orbitonasalis has grown further in size. Its lower half is in the form of a pillar, the upper half is considerably expanded. This expanded portion shows three processes or projections: two on the anterior edge and one on the postero-

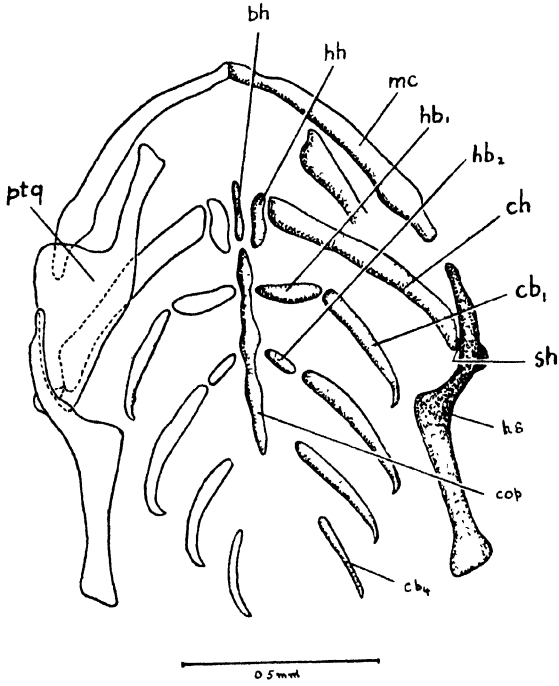

FIG. 7.—*Notopterus chitala*—Stage C, 14 mm. long. Dorsal view of the visceral arches. Pterygo-quadrate of the right side partly removed.

dorsal edge. Dorsally the lamina is greater in height than the upper edge of the pre-optic root (fig. 10) except in the region of the posterior process of the lamina where they are level. The entire medial surface of the lamina orbitonasalis is fused with the lateral surface of the pre-optic root except in the areas of the three projections mentioned above and in a narrow longitudinal area along the remaining dorsal margin of the pre-optic root. In fig. 10 the shaded area represents the extent of the fusion of the lamina and the pre-optic root.

Two passages are present between the orbit and the ethmoid region. The first, which is dorsal, runs between the upper margin of the lamina orbitonasalis and the pre-optic root. It will be seen from fig. 10 that this passage is not a well defined canal surrounded on all sides by cartilage. Posteriorly it has neither cartilaginous floor nor roof, the lateral wall is provided by the dorso-posterior process of the lamina

orbitonasalis and the medial wall by the pre-optic root (T.S. at I–J). In front of this region the lateral wall of the passage consists of the lamina orbitonasalis: the floor is provided by the fusion of the pre-optic root with the lamina: to a slight extent the medio-ventral wall is provided by the upper edge of the pre-optic root, the greater area of the medial wall is membranous consisting of the dura mater: there is no cartilaginous roof (T.S. at G-H). In the anterior region of the passage the lateral wall consists of the upper anterior process of the lamina orbitonasalis: there is a cartilaginous floor in half of the length of this process: the medial wall is partly cartilaginous, consisting of the upper edge of the pre-optic root, and partly membranous provided by the dura mater. Through this dorsal passage the nasal vein and the ophthalmic branch of the fifth nerve gain entry to the nasal fossa from the orbit. The seventh ophthalmic nerve runs dorsally to this passage.

The second passage is ventral to the lower edge of the pre-optic root. The floor of this passage is provided by the trabecula (T.S. at E-F), the lateral wall by the pillar of the lamina orbitonasalis, the roof by the thickness of the cartilage of the lower edge of the pre-optic root (which is here fused to the lamina orbitonasalis), and the medial wall by the dura mater. The orbitonasal artery and a vein run through this passage from the orbit to the nasal sac. The passage is small and

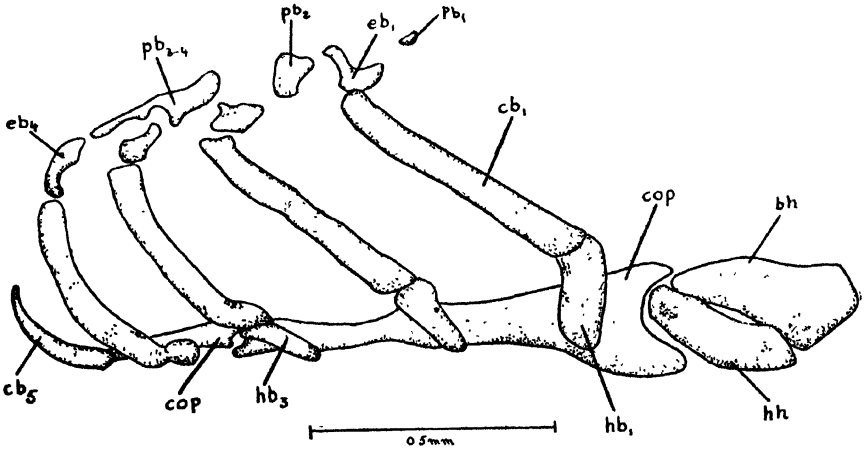

FIG. 8.—*Notopterus chitala*—Stage E, 17 mm. long—Lateral view of the visceral arches. The mandibular arch and the upper elements of the hyoid arch are not shown.

there is no cavum orbitonasale since the pre-optic root is fused to the lamina orbitonasalis. The pre-optic roots of both sides are wide apart: hence there is no interorbital septum. The olfactory foramen (evehens) is anterior to the lamina orbitonasalis.

The trabecula of each side has become discontinuous because of the absorption of cartilage in part of its length (fig. 9). Except for the pre-optic root, taenia marginalis and postorbital process, the remaining side wall of the skull is membranous (fig. 10), consisting of dura mater heavily reinforced by connective tissue fibres. The membranous side wall on each side stretches from the lower edges of the elements of the orbital cartilage towards the trabecula in an oblique (ventro-medial) direction. The membrane touches the medial edge of the trabecula and then stretches in the space (i.e. the hypophysial fenestra) between the trabeculae of the two sides. The dorsal surface of the trabecula thus constitutes a sub-ocular shelf.

Unlike the pre-optic root and the taenia marginalis, which are closely attached to the dura mater, the postorbital process is attached only in part of its medial surface. Only the medial surface of the anterior finger-like projection and the upper

portion, consisting of about one-third of the breadth of the plate of the postorbital process, are closely attached to the dura mater. The lower two-thirds of the plate bend laterally away from the dura mater. An epidural but intra-mural longitudinal passage, ventrally and anteriorly confluent with the orbit, is thus provided through the upper portion of which run the V and VII ophthalmic nerves (fig. 12). In this part of their course, therefore, these nerves, though medial to the plate of cartilage, do not traverse the true cranial cavity, which is delimited by the dura mater. It is evident that in the lower zone of the postorbital process a duplication of the side wall has taken place—the inner wall being membranous, the outer cartilaginous. In a later stage (20 mm) the inner membranous wall also becomes chondrified to some extent by the posterior growth of the taenia marginalis (fig. 11) These relations show that the lower part (lateral to the nerves) of the plate of cartilage is not strictly speaking a part of the postorbital process (which is restricted to the upper part of the plate only) but is the anterior extension of the crista parotica. This extension, instead of being a ridge has become modified into a thin plate. From

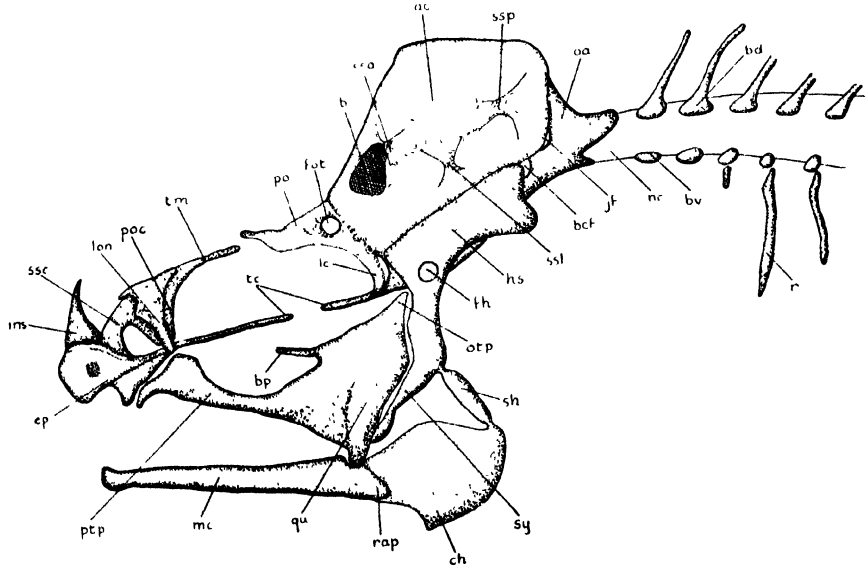

FIG. 9.—*Notopterus chitala*—Stage F, 18 mm. long—Lateral view of the neurocranium and a part of the visceral arches.

the very beginning, the postorbital process and the anterior extension of the crista parotica develop fused to each other—the ventral edge of the process fused to the dorsal edge of the crista. Since the part of the postorbital process medial to the crista does not chondrify for a long time, the crista parotica appears to be a part of the postorbital process, and can only be recognized by its relation to the nerves.

The anterior tip of the notochord is slightly behind the posterior edge of the pro-otic bridge. Except in the posterior region near the posterior basicapsular commissure, in the remaining part of their length behind the pro-otic bridge the parachordals are still separated by the notochord. Seen in transverse sections the parachordals of each side in this region have a thick semilunar outline, disposed in such a way that the convex surfaces of the parachordals of both sides support the notochord between them. The lower, concave, margin slants away ventro-laterally.

In the posterior region each parachordal is reduced to a strip of cartilage which supports the ventro-lateral area of the notochord. The lateral aspect of the

notochord is not covered by cartilage. Posteriorly the parachordals run into the posterior basicapsular commissure, which is very thick and supports the lateral aspect of the notochord. A median longitudinal strip of cartilage extends over the dorsal surface of the notochord in the region of the thin parachordals. Posteriorly this median strip is fused to the anterior end of the dorso-median edge of the thick posterior basicapsular commissure. A plate of cartilage extends between the dorso-lateral margin of this strip of cartilage and the medial aspect of the inturned posterior wall of the auditory capsule. The posterior edge of this plate is fused with the anterior dorsal edge of the basicapsular commissure. The result of all this is that a chamber is formed in which the lagena is lodged. The medial wall of this chamber is provided by the notochord, the medio-ventral area by the parachordal, the floor by the membrane covering the basicapsular fenestra, the lateral wall consists partly of the continuation of this membrane and partly of the cartilage of the floor of the auditory capsule; the roof is furnished by the above-mentioned plate of cartilage. The hind wall of the chamber is provided by the thickness of the basicapsular commissure. Anteriorly the chamber is confluent with the depression lodging the

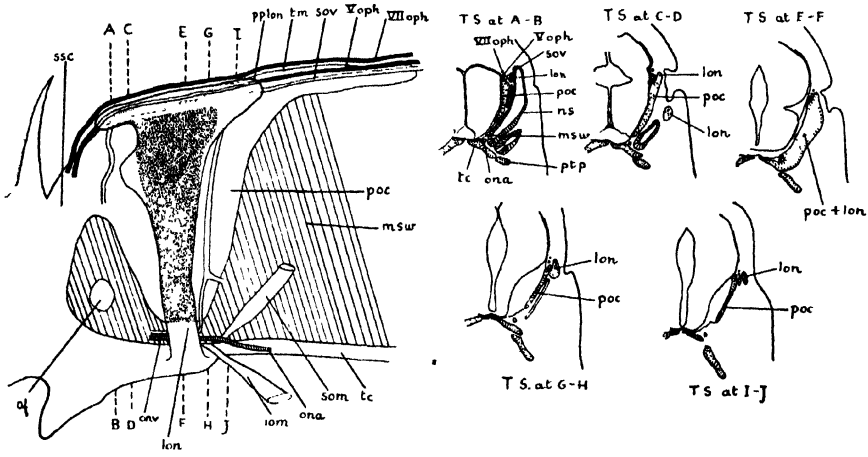

FIG. 10.—*Notopterus chitala*—Stage F, 18 mm. long—Diagram showing the relations of the lamina orbitonasalis to the pre-optic root of the orbital cartilage and to the neighbouring blood-vessels. In the figure showing the lateral view of these structures the shaded part indicates the actual area of the fusion of the lamina orbitonasalis with the pre-optic root.

saccule. Ventrally to the latero-ventral area of the membranous wall of this chamber will extend the anterior diverticulum of the air-bladder. In this stage the diverticulum has not reached underneath the membrane, but extends only below the occipital arch. In the 20 mm. stage it has grown further forwards reaching underneath the chamber.

Stage G. 20 mm. long.

This is the oldest stage in the collection. The pre-optic root has become quite extensive (fig. 11). It is still free from the trabecula. The median spine growing from the upper posterior edge of the internasal septum has now grown further backwards extending over the region of the lamina orbitonasalis. This spine or slender bar of cartilage is the taenia tecti medialis anterior. Except for the tectum synoticum it is the sole element yet developed in the roof of the chondrocranium. The taenia marginalis has grown posteriorly close to the membranous side wall and medially to the plate-like crista parotica as explained above. In figure 11 the upper dotted line under the postorbital root indicates the upper edge of the taenia marginalis. This edge is fused with the postorbital root.

The trabeculae have been absorbed in the greater part of their length and behind the ethmoid plate they do not form a trabecula communis, though both have come very near to one another. The posterior half of the auditory capsule is roofed over by a thin tectum synoticum. A median process extends from the anterior edge of this tectum. No tectum posterius is developed.

The basal process of the pterygo-quadrate is very well developed and its anterior part is broad and plate-like. The anterior end of the pterygoid process is articulated by means of the ethmo-palatine and rostro-palatine articulations to the trabecula. The retroarticular process of Meckel's cartilage is strongly developed. The lower end of the symplectic is medial to the quadrate, but is not fused with it.

In the branchial arches the fused pharyngo-branchials of the third and fourth arches have now become separated into distinct cartilages. The first three branchial arches have separate pharyngo- epi- cerato- and hypobranchials. The fourth arch consists of separate pharyngo- and epi-branchials and fused cerato- and hypobranchials. In the fifth arch only the cerato-branchial is represented. From the posterior edge of each epi-branchial a process is given out which projects towards the pharyngo-branchial of the arch behind. The process of the epi-branchial of the fourth arch is recurved posteriorly and forms a ring. The copula is segmented into two pieces. The anterior piece is long and narrow and extends from behind the first to the third branchial arch. The posterior piece is short and broad and extends to the last two arches.

3. Relations to the Cartilages of the chief Nerves, Blood-vessels and Muscles.

In the 20 mm. larva the m. obliquus superior is attached between the dorso-medial surface of the trabecula and the membranous side wall below the base of the pre-optic root. The attachment is behind the lamina orbitonasalis. The m. obliquus inferior is attached at the posterior opening of the orbito-nasal passage. This passage is small in size and the muscle does not actually enter it to gain a position on the medial side of the lamina orbitonasalis. Thus there is practically no anterior myodome. The internal, superior and inferior rectus muscles are attached to the sub-ocular shelf at an area situated at the beginning of the posterior one-third of the length of the trabecula. The posterior or external rectus muscle is similarly attached to the sub-ocular shelf, but this attachment is a short distance behind that of the other rectus muscles. There is no posterior myodome.

The infundibulum is very big and is pressed downwards and occupies the depression formed by the medial margins of the trabeculo-parachordal junction in front of the pro-otic bridge. This posterior region of the hypophysial fenestra of *Notopterus* has a structural resemblance to the anterior part (so-called dorsal part) of the posterior myodome of *Salmo*. The posterior myodome of *Salmo* consists of three regions (de Beer, 1937, p. 127): (1) the anterior portion in front of the pro-otic bridge, (2) the middle portion under the pro-otic bridge, (3) the posterior portion in the form of a groove on the ventral side of the basal plate. In larval *Notopterus* the middle and posterior portions of the myodome of *Salmo* are represented by very small spaces lying below the pro-otic bridge and parachordals and above the parasphenoid bone. Thus the only portion of the myodome of *Salmo* represented to some extent in *Notopterus* is the anterior portion. This depression of *Notopterus* cannot be called a myodome since it is not a subdural space lodging the eye-muscles but houses an extension of true cranial space as the dura mater is pressed down in its cavity by the infundibulum.

A trigemino-facialis chamber is present in which the pars ganglionaris and the pars jugularis are confluent. The lateral wall of the chamber is formed by the lateral commissure. Through the hinder opening of this chamber (between the lateral commissure and the anterior basicapsular commissure) the hyomandibular facialis nerve and the head vein emerge and the orbital artery enters the chamber (fig. 12). The anterior aperture of the trigemino-facialis chamber opens widely

into the orbit and through it pass out the palatine, buccalis facialis and the branches of the trigeminal nerve. The head vein, running antero-posteriorly, enters the chamber through the same opening. The head vein is medial to the trigeminal ganglion and lateral to the facial ganglion within the chamber. The hyomandibularis facialis after emerging from its ganglion runs backwards ventrally to the head vein. Posteriorly the head vein runs between the head of the hyosymplectic and the auditory capsule dorsally to the adductor hyomandibularis muscle. The head vein passes laterally to the glosso-pharyngeal nerve and medially to the vagus. Anteriorly the head vein is formed by the union of the superior and inferior orbital veins. The superior orbital vein in its turn is formed by the union of two veins which drain blood from the ethmoid region (fig. 10).

The internal carotid arteries passing ventrally to the trabeculae enter the cranial cavity through the hypophysial fenestra, but just before doing so, they come into contact with the efferent pseudo-branchial arteries, which, running from the pseudobranch, also pass ventrally to the trabeculae. The continuation of the efferent pseudobranchial artery is the arteria ophthalmica magna, which passes out dorsally to the trabecula.

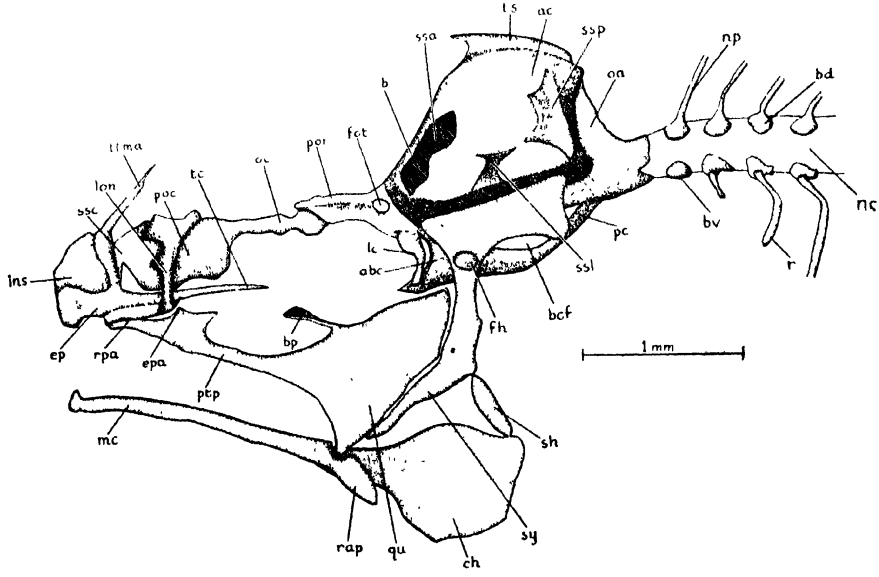

FIG. 11.—*Notopterus chitala*—Stage G. 20 mm. long—Lateral view of the neurocranium and a part of the visceral arches.

The afferent pseudobranchial artery is medioventral to the upper, posterior tip of the quadrate: therefore this portion of the quadrate represents a rudimentary otic process. Before reaching the pseudobranch the afferent pseudobranchial artery rising high up runs externally to the orbito-nasal artery. A commissural vessel exists between the orbital artery and the afferent pseudobranchial. The pseudobranch has lost all connection with the pharyngeal epithelium and is deeply buried in connective tissue almost at the level of the trabecula. (In figure 12 it is shown pulled down for the sake of clarity.) It has a spherical shape and seems to correspond to the ' glandular ' type of pseudobranch found in some Teleostei.

Two arteries, the orbital and the orbito-nasal, are given off by the internal carotid artery before it enters the skull. The former enters the trigemino-facialis chamber through its posterior opening and, inside the chamber, runs laterally to the facial

ganglion. The orbital artery runs forward medially to the main branches of the trigeminal nerve and to the buccalis facialis. The orbito-nasal artery passes over the junction of the lateral commissure and the trabecula. This artery is not enclosed here in a foramen as it is, together with the palatine nerve, in *Salmo* (de Beer 1927). The orbito-nasal artery continues its way through the orbit passing medially to the main trigeminal branches and buccalis facialis and ventrally to the arteria ophthalmica magna and all the eye-muscles, except the inferior oblique to which it is dorsal (fig. 10). Eventually it enters the orbito-nasal passage as already described.

The palatine nerve after emerging from the anterior opening of the trigemino-facialis chamber passes medially to the orbito-nasal artery and runs, first externally and then ventrally to the trabecula.

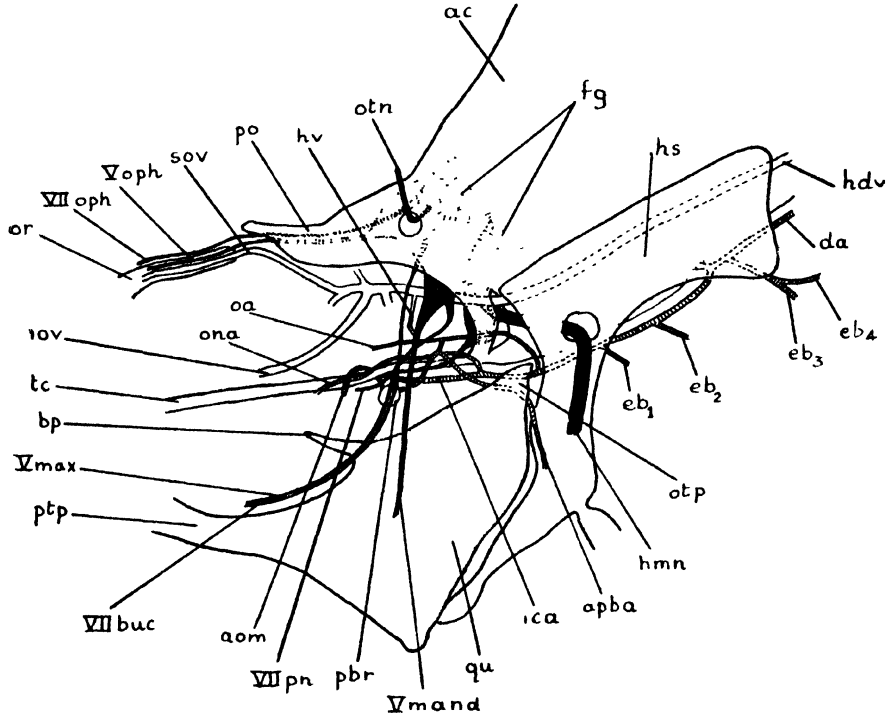

FIG. 12.—*Notopterus chitala*.—The relations of the chief nerves and blood-vessels to the cartilages of the chondrocranium.

The relations of the V and VII ophthalmic nerves to the side wall of the skull have already been explained in the preceding part. The relations of the n. buccalis facialis and the maxillary and mandibular branches of the fifth nerve are self-evident from fig. 12. and therefore do not require any detailed description. Two points should, however, be noted regarding these nerves. The maxillary and mandibular branches of V have a peculiar relation to each other. The maxillary branch instead of leaving the trigeminal ganglion antero-dorsally to the mandibular branch leaves the ganglion postero-ventrally to it, then crosses the mandibular branch medially and runs forwards and downwards. At the point of intersection there seems to be some exchange of fibres between these two nerves. The second point to be noted is that the n. buccalis facialis leaves the facial ganglion high up, behind the oticus

facial foramen and then runs down anteriorly to the pituitary vein and the mandibular branch of the fifth ; it passes laterally to the maxillary branch and then runs along ventrally to this nerve. Both these nerves pass dorso-laterally over the basal process.

The glossopharyngeal nerve, coming from the brain, passes between the utriculus and the sacculus (medially to utriculus and laterally to sacculus) behind the utriculosaccular junction. Here, while the nerve is still inside the auditory cavity, the supratemporal branch separates from the main nerve, which soon pierces its foramen through the base of the capsule. The supratemporal branch on the other hand runs posteriorly along and underneath the posterior ampulla and the lower part of the posterior semicircular canal to enter the canal or cavity in the cartilage of the auditory capsule, which lodges the semicircular canal behind the septum semicirculare posterius. The nerve eventually enters a foramen through the base of this cavity.

4. Conclusions.

The description of the chondrocranium of *Notopterus* shows that the embryonic skull of this fish closely resembles that of *Salmo*. Among the chief differences between *Notopterus* and *Salmo* is the absence of myodomes in larval *Notopterus*. In *Salmo* an elaborate anterior myodome is developed, with the result that an interorbital septum and cavum orbito-nasale are formed, the olfactory nerve passing through two foramina—evehens and advehens—since it traverses a part of the orbit. In *Notopterus* this region is very simple : the lamina orbito-nasalis has not shifted anterior to the foramen olfactorium evehens, no cavum orbito-nasalis is formed and the pre-optic roots are not fused into any interorbital septum but remain separate and wide apart and fused to the lamina orbito-nasalis. Similarly the region of the trabeculo-parachordal junction in front of the pro-otic bridge is simplified because of the absence of any functional posterior myodome.

In *Salmo* an independent orbital cartilage appears which, later on, fuses anteriorly with the lamina orbito-nasalis and internasal septum and posteriorly with the auditory capsule. The partly-fused pre-optic roots develop late. In *Notopterus* on the other hand the separate pre-optic roots appear quite early, and so does the postorbital process from the auditory capsule. No independent orbital cartilage (or taenia marginalis) develops, but it grows as a posterior extension of the preoptic root and then fuses with the postorbital process. The shape and relations of the crista parotica to the postorbital process and to the ophthalmic nerves as described above are interesting and are not present in *Salmo*. The basal process of *Notopterus* is better developed than that of *Salmo*. It does not however reach near the neurocranium. A basitrabecular process is not developed. Apart from these differences, the chondrocranium of *Notopterus* is very much like that of *Salmo*.

When compared with the chondrocranium of *Gymnarchus*, that of *Notopterus* does not show any close similarity to it. In *Gymnarchus* the orbital cartilage is so well developed that it furnishes the complete side wall of the orbitotemporal region, a pila antotica secundaria is present, the lamina orbito-nasalis is rudimentary, the nasal sacs are small and far removed from the thick internasal septum, the roof is fairly well developed and the pterygoquadrate is fused to the hyomandibula. In *Notopterus*, on the other hand, the orbital cartilage is not so well developed, and is in no way different from other Teleostei where the side wall is rudimentary and there is no pila antotica secundaria ; the lamina orbito-nasalis is well developed, the nasal sacs are large and close to the internasal septum, the roof is very poorly developed, the pterygoquadrate is not fused with the hyosymplectic. Moreover the relations of the nerves and blood-vessels to the cartilages in *Notopterus* are very similar to *Salmo* and not in any way like those of *Gymnarchus*. The peculiar dorsal cutaneous facialis nerve is confined to *Gymnarchus* alone (Omarkhan, 1949), neither is the splitting of the common truncus hyomandibularis into two quite independent nerves, as in *Gymnarchus*, found in *Notopterus*.

To sum up, this study shows that the embryonic skull of *Notopterus* more closely approaches the generalized clupeiform chondrocranium of *Salmo* than that of the specialized *Gymnarchus*. This is interesting, since Ridewood (1904) who investigated the adult bony skulls of the Mormyridae, Hyodontidae and Notopteridea came to this conclusion: "... the families Mormyridae, Notopteridae and Hyodontidae, though more closely related *inter se* than is either family with any other family of Malacopterygian fishes, are not more intimately related with one another than was previously assumed to be the case. ..."

The bony skull of *Notopterus*, therefore, does not resemble the skull of *Salmo* so much as the skull of *Gymnarchus*, but the chondrocranium of *Notopterus* resembles the chondrocranium of *Salmo* more than it does that of *Gymnarchus*.

5. Summary.

The development of the chondrocranium of *Notopterus* is described and compared with those of *Salmo* and *Gymnarchus*. This study shows that, in this respect, *Notopterus* has no close resemblance to *Gymnarchus* but is more like the generalized clupeiform chondrocranium of *Salmo*, although according to Ridewood the adult skulls of *Notopterus* and *Gymnarchus* are closer to each other than to *Salmo* or any other teleost.

In the chondrocranium of *Notopterus* the myodomes are absent. There is no interorbital septum. A large pre-optic root is fused to the lamina orbito-nasalis. There are neither pila antotica secondaria nor metoptic root. The pterygoquadrate is not fused to the hyosymplectic. The anterior diverticulum of the air-bladder is not lodged within the cavity of the auditory capsule but touches the base of the capsule.

Relations of the arteries, veins and nerves to the cartilages are described. A normal teleostean common truncus hyomandibularis is present.

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7. Explanation of Lettering.

V.mand n. mandibularis trigeminus; *V.max* n. maxillaris trigeminus; *V.oph* n. ophthalmicus superficialis trigeminus; *VIIbuc* n. buccalis facialis; *VIIoph* n. ophthalmicus superficialis facialis; *VIIpm* n. palatinus facialis.

abc anterior basicapsular commissure; *ac* auditory capsule; *aom* arteria ophthalmica magna; *apba* afferent pseudobranchial artery.

b part of intertemporal bone covering the space in the wall of the auditory capsule; *bcf* basicapsular fenestra; *bd* basidorsal; *bh* basihyal; *bp* basal process; *bv* basiventral.

cb$_{1-5}$ ceratobranchials 1 to 5; *ch* ceratohyal; *cop I-II* first and second copula.

da dorsal aorta.

eb$_{1-4}$ efferent branchial arteries 1 to 4; *ep* ethmoid plate; *epa* ethmo-palatine articulation.

fg facial ganglion; *fh* foramen in hyosymplectic for hyomandibular nerve; *fot* foramen for VII otic nerve.

gf foramen for glossopharyngeal nerve.

hb$_{1-3}$ hypobranchials 1 to 3; *hdv* head vein; *hf* hypophysial fenestra; *hp* hypohyal; *hmn* hyomandibular facial nerve; *hs* hyosymplectic; *hv* hypophysial vein.

ica internal carotid artery; *ins* internasal septum; *iom* inferior oblique muscle; *iov* inferior orbital vein.

jf jugular or metotic foramen.

lc lateral commissure; *lon* lamina orbito-nasalis.

mc Meckel's cartilage; *msw* membranous side wall.

nc notochord; *ns* nasal sac.

oa occipital arch; *oar* orbital artery; *of* olfactory foramen; *ona* orbito-nasal artery; *onv* orbito-nasal vein; *or* orbital cartilage; *otn* VII otic nerve; *otp* otic process.

pb_{1-4} pharyngobranchials 1 to 4; *pbc* posterior basicapsular commissure; *pbr* pseudobranch; *po* postorbital process; *poc* pre-optic root of orbital cartilage *poc+lon* fused pre-optic root and lamina orbito-nasalis; *por* postorbital root; *pplon* posterior process of lamina orbito-nasalis; *pb* pro-otic bridge; *ptb* pterygoid process of quadrate; *ptq* pterygoquadrate; *pwac* posterior wall of auditory capsule.

qu quadrate.

r rib; *rap* retro-articular process; *rps* retro-palatine articulation; *rprb* rudiment of pro-otic bridge.

sh stylohyal; *som* superior oblique muscle; *sov* superior orbital vein; *ssa* septum semicirculare anterius; *ssc* sphenoseptal commissure; *ssl* septum semicirculare laterale; *ssp* septum semicirculare posterius; *sy* symplectic part of hyosymplectic.

tc trabecula cranii; *tm* taenia marginalis; *ts* tectum synoticum; *ttma* taenia tecti medialis anterior.

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